UNIVERSITÉ DU QUÉBEC À MONTRÉAL

SHOOT AND ROOT RESPONSES OF HYBRID POPLARS TO INTERSPECIFIC COMPETITION AND SOIL FERTILITY

DISSERTATION

PRESENTED AS

PARTIAL REQUIREMENT

OF THE DOCTORATE OF ENVIRONNEMENTAL SCIENCES

BY

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OCTOBER 2011

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

RÉPONSE DE LA TIGE ET DES RACINES DU PEUPLIER HYBRIDE À LA COMPÉTITION INTERSPÉCIFIQUE ET LA FERTILITÉ DES SOLS

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

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OCTOBRE 2011

REMERCIEMENTS

Ce travail de recherche a été rendu possible par le soutien technique et financier de Ressources Naturelles Canada (RNCAN), du Fonds québécois de recherche sur la nature et les technologies (FQRNT) via une subvention de recherche accordée à C. Messier et une bourse doctorale accordée au candidat, de l'Université du Québec à Montréal (UQAM) via les bourses d'excellence FARE, ainsi que du Réseau Ligniculture Québec (RLQ). Des remerciements particuliers à chaque chapitre de la thèse se retrouvent aux sections correspondantes.

Je dois souligner l'indispensable contribution de mes superviseurs, David Paré (directeur, RNCAN) et Christian Messier (co-directeur, UQAM), qui ont cru en moi, m'ont encouragé, m'ont poussé à me dépasser, tout en me laissant une grande liberté. Ce fut un honneur et un plaisir de travailler avec ces grands hommes. Je suis aussi très reconnaissant de la généreuse collaboration des autres membres de mon comité d'encadrement qui ont apporté leur savoir et leur expérience dans la mise en œuvre de ce projet : Nicolas Bélanger (TELUQ) et Annie DesRochers (UQAT). Pierre Gagné et Brigitte Bigué du RLQ ont également fourni un appui essentiel. Merci à tous.

Mes pensées vont aussi à mes parents pour leur soutien indéfectible, leur exemple inspirant, et leur contribution primordiale à ce que je suis aujourd'hui; à ma famille élargie, à mes amis, et bien sûr à ma tendre épouse Marie-Ève, qui fut à la fois mon admiratrice et ma critique no.1, et sans qui ce bateau aurait été bien vide.

AVANT–PROPOS

Ce projet de recherche doctorale a été divisé en trois chapitres, conçus sous le format d'articles de revue scientifique. Le premier a été publié dans la revue *Forest Ecology and Management* (Bilodeau-Gauthier, Simon, David Paré, Christian Messier, Nicolas Bélanger. 2011. For Ecol Manag. 261(3):620-629.). Le second regroupe les mêmes auteurs que le premier, tandis que le troisième sera signé par S. Bilodeau-Gauthier, D. Paré, et C. Messier. Ces deux derniers articles seront soumis à des revues telles que *Plant and Soil, Journal of Experimental Botany* ou *Journal of Applied Ecology*. Ces trois chapitres sont présentés ici intégralement, dans leur version en langue anglaise. Ils sont accompagnés d'une introduction et d'une conclusion générales rédigées en français et visant à relier les chapitres entre eux afin de former un tout cohérent.

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RÉSUMÉ

Un zonage forestier incluant une sylviculture intensive d'arbres à croissance rapide sur une portion restreinte du territoire permettrait de répondre à la demande pour les produits du bois, réduire la pression sur les forêts naturelles, et augmenter la superficie d'aires protégées. Le peuplier hybride constitue un excellent candidat à la sylviculture intensive puisque sa croissance permet une récolte après 20 ans. Cette étude avait pour objectif d'évaluer les conditions environnementales qui optimisent la croissance du peuplier hybride en sol forestier boréal. Trois techniques d'aménagement sylvicole (la préparation mécanique du sol, le contrôle de la compétition végétale, et la fertilisation) ont été testées sur 40 hectares de plantations dans la région du Saguenay–Lac-Saint-Jean. Des excavations de systèmes racinaires de peupliers, accompagnées d'incubations de sol à différentes profondeurs, ont été effectuées pour expliquer la réponse aux techniques d'aménagement. La compréhension du comportement des racines du peuplier a été approfondie par une expérience en pots, où des peupliers ont été plantés en présence de graminées et avec une distribution spatiale des nutriments homogène ou hétérogène. Les résultats suggèrent de favoriser la préparation mécanique du sol avant les autres techniques d'aménagement sylvicole puisqu'elle offre les meilleurs gains en croissance. La préparation par monticules s'avère être la meilleure méthode pour assurer la survie et la croissance des peupliers. Le développement du système racinaire est en effet grandement favorisé dans les monticules grâce au sol plus chaud et plus meuble, à une minéralisation accrue de l'azote, et à une faible compétition racinaire, ce qui donne accès à un large volume de sol et à un important réservoir de nutriments. Les racines de peupliers évitent effectivement la compétition, et ce, même à leur détriment, quand les zones les plus fertiles du sol sont occupées par la compétition. Pourtant, les résultats de l'expérience en pots démontrent que le peuplier peut malgré tout pénétrer dans la zone d'un compétiteur, si cette dernière est au moins aussi fertile que la sienne. Les racines de peuplier ont exploré davantage le sol et accédé ainsi à plus de ressources, malgré la présence de compétition, quand la distribution des nutriments était homogène. La croissance de la tige est dans ce cas semblable aux traitements sans compétition. Le peuplier réagit à la compétition et à la distribution spatiale des nutriments en modifiant son architecture racinaire, ce qui témoigne de sa grande plasticité. Cette étude favorisera le succès des plantations de peupliers hybrides, une condition gagnante du zonage forestier, en plus de générer des connaissances nouvelles pour mieux comprendre le comportement des plantes.

Mots-clés : aménagement sylvicole, azote, compétition végétale, distribution spatiale des nutriments, fertilisation, peuplier hybride, plantation d'arbres à croissance rapide, préparation mécanique du sol, racines, sols forestiers.

ABSTRACT

A forest zoning approach that includes intensive silviculture of fast-growing trees on a restricted portion of the territory would meet the demand for wood products, reduce the pressure on natural forests, and increase the surface of protected areas. Hybrid poplar is an excellent candidate for intensive silviculture as its fast growth allows harvest after 20 years. This study aimed to assess environmental conditions that maximize the growth of hybrid poplars in boreal forest soils. Three silvicultural techniques (mechanical soil preparation, vegetation control, and fertilization) were tested on 40 hectares of plantations in the Saguenay-Lac-Saint-Jean region. Excavations of root systems of poplars, along with incubations of soil at different depths, were conducted to explain the response to management techniques. The understanding of the behavior of hybrid poplar roots was deepened through a pot experiment where poplars were planted in the presence of grass and with a varying spatial distribution of nutrients, either homogeneous or heterogeneous. The results suggest that mechanical soil preparation should be promoted before the other forest management techniques since it provides the best gains in growth. The mounding preparation proves to be the best method to ensure the survival and growth of hybrid poplar trees. The development of the root system was greatly favored in the mounds due to the soil that was warmer and looser, the increased mineralization of nitrogen, and the low root competition, which provided access to a large volume of soil and an important source of nutrients. Poplar roots actively avoided competition, even to their detriment when the most fertile areas of land were occupied by live competitors. Yet the results of the pot experiment showed that poplar roots could still enter the soil area occupied by a competitor, if it was at least as fertile as its own starting soil area. Poplar roots explored the soil further and gained more resources, despite the presence of competition, when the nutrient distribution was homogeneous. Stem growth in this case was similar to the treatments without competition. Hybrid poplars respond to the presence of competition and the spatial distribution of nutrients by modifying root architecture, reflecting its high plasticity. This study will promote the success of hybrid poplar plantations, a winning condition of forest zoning, in addition to generating new knowledge to better understand the behavior of plants.

Keywords : silviculture, nitrogen, plant competition, spatial nutrient distribution, fertilization, hybrid poplar, fast-growing tree plantation, mechanical soil preparation, roots, forest soils.

INTRODUCTION

1.1 Mise en contexte

Cette première section de la thèse sert à dresser la table pour la lecture des trois chapitres suivants qui constituent les résultats de la recherche. Tout d'abord, la problématique, d'un point de vue international, puis, plus spécifiquement d'un point de vue québécois, sera présentée. Elle sera suivie de l'objectif de recherche et de la justification de la pertinence scientifique de la recherche. La pertinence de la recherche s'articule autour de quatre axes : 1) l'étude du peuplier hybride comme un cas d'espèce, 2) l'importance d'étudier le peuplier hybride en sol boréal, 3) celle d'étudier la combinaison de différentes méthodes d'aménagement sylvicole, puis 4) l'apport d'une recherche portant spécifiquement sur les racines. Un état des connaissances sera ensuite présenté. Il portera sur : l'aménagement des plantations, la compétition végétale et les racines. Pour clore cette section, un plan de la thèse décrira brièvement chacun des chapitres qui suivent, et finalement, un tableau synthèse permettra de voir en un coup d'œil les objectifs spécifiques et généraux de chacun des chapitres, ainsi que les thèmes qu'ils abordent.

1.1.1 À l'échelle internationale

À l'heure actuelle, scientifiques, industriels et écologistes s'entendent sur l'importante diminution des forêts anciennes, et ce, à travers le monde. L'appétit des compagnies forestières pour la ressource, partout où elle se trouve, ne cesse d'augmenter, tout comme le désir des consommateurs pour les nombreux produits issus du bois. De plus en plus conscients des problèmes que cette pression exerce sur l'écosystème, de nombreuses voix s'élèvent pour réclamer un aménagement durable des forêts, particulièrement dans les régions où l'industrie forestière occupe une place importante, comme le Canada, les États-Unis, l'Union Européenne et l'Amazonie.

C'est pourquoi certains scientifiques prônent une approche différente : celle du zonage forestier (Messier et Kneeshaw, 1999 ; Messier *et al.*, 2009b ; Seymour et Hunter, 1992). Selon cette approche, l'utilisation de plantations d'arbres à croissance rapide sur une portion restreinte du territoire permettrait de réduire la pression sur les forêts naturelles (Paquette et Messier, 2010), d'augmenter les surfaces allouées aux aires protégées et à l'aménagement écosystémique (Başkent et Yolasığmaz, 2003), tout en maintenant ou même en stimulant la production ligneuse (Binkley, 1997 ; Fox, 2000 ; Messier *et al.*, 2003).

Dans ce contexte, le peuplier hybride – arbre à la croissance très rapide et objet de cette recherche doctorale – s'avère d'un grand intérêt puisqu'il peut être récolté après 20 ans seulement. Les rendements de plantations à rotations courtes sont le fruit de programme d'amélioration génétique et de techniques d'aménagement sylvicole intensif (Ceulemans et Deraedt, 1999 ; Ceulemans *et al.*, 1992 ; Strobl, 1987). Dans plusieurs régions du monde, la principale espèce arborée à croissance rapide appartient justement au genre *Populus* (Christersson, 2006 ; Pontailler *et al.*, 1999 ; Rodríguez *et al.*, 2010). Cependant, les espèces, clones et hybrides de *Populus* sont très exigeants en matière de nutriments, d'eau et de lumière (Barnéoud *et al.*, 1982 ; Mitchell *et al.*, 1999 ; Paré *et al.*, 2001).

Il n'est toutefois pas suffisant de planter des arbres à croissance rapide, il faut aussi bien choisir les endroits où les installer. En effet, les cas d'insuccès de plantations d'espèces d'arbres à croissance rapide sont souvent attribuables à une mauvaise sélection des pratiques d'aménagement du sol (Evans, 1999). Jusqu'à aujourd'hui, la grande majorité des plantations de peupliers hybrides sous les latitudes nordiques, par exemple en Suède (Christersson, 2008, 2010), ou dans la région transitoire entre les prairies et la forêt boréale du centre du Canada (Amichev *et al.*, 2010 ; Block *et al.*, 2009 ; Pinno et Bélanger, 2009 ; Pinno *et al.*, 2009), se retrouve sur des terres agricoles. Seule une minorité de plantations ont été tentées sur des sites forestiers dans l'est du Canada (Bona *et al.*, 2008 ; Coll *et al.*, 2007 ; Guillemette et DesRochers, 2008 ; Sigouin, 2008). Considérant la demande accrue pour l'accès aux terres agricoles et les conflits d'usage en découlant, il est probable que de futures plantations à croissance rapide soient établies sur des sites forestiers. Étant donné l'étendue de la forêt

boréale dans l'hémisphère Nord, il apparaît d'autant plus pertinent de s'attarder aux sites forestiers boréaux.

L'approche du zonage forestier propose donc une solution de rechange particulièrement intéressante à la manière traditionnelle de récolter la ressource forestière. Les plantations de peupliers hybrides font certainement partie de cette approche novatrice. Cependant, comme elles ne connaissent pas le même succès partout, notamment en raison des types de sol où elles ont été tentées, il est important de poursuivre la recherche concernant cette approche, cette espèce d'arbre et les conditions dans lesquelles elle est cultivée.

1.1.2 Cas du Québec

Le Québec est une province canadienne particulièrement choyée par l'étendue de sa forêt, qui couvre 760 000 km^2, soit la moitié de son territoire, ce qui représente 20 % des forêts du Canada et 2 % de celles de la planète (MRNFQ, 2009). La récolte du bois occupe une place importante dans l'économie québécoise et a grandement contribué, pendant des décennies, au développement de régions éloignées de la métropole de Montréal, notamment l'Abitibi, le Saguenay-Lac-Saint-Jean, la Côte-Nord, le Bas-Saint-Laurent et la Gaspésie (e.g., Boucher *et al.*, 2009 ; Pinna *et al.*, 2009). Le Québec s'est longtemps considéré comme riche de ces ressources qui apparaissaient, jusqu'à pas si longtemps encore, inépuisables.

L'alarme a été sonnée en 1999 par le documentaire-choc *L'Erreur boréale* de Richard Desjardins et Robert Monderie. Cette cinglante remise en question des pratiques forestières a eu d'importants échos dans les médias et a grandement troublé une partie de la population ignorante de ces pratiques. Le documentaire a été l'élément déclencheur d'une série d'événements et de décisions politiques au Québec. En 2002, un rapport de la vérificatrice générale a reconnu que le Ministère des Ressources naturelles du Québec n'était pas en mesure d'estimer clairement le niveau d'exploitation des forêts de la province. Une commission d'étude – couramment appelée Commission Coulombe, du nom de son commissaire principal – a ensuite été mise sur pied afin d'évaluer la gestion de la forêt publique québécoise. Elle a livré un désolant constat dans son rapport de 2004 : la forêt avait

été surexploitée depuis des décennies. La Commission est allée jusqu'à recommander une baisse immédiate de 20 % de la possibilité de récolte forestière.

Le gouvernement du Québec a réagi en 2008 avec un *Livre vert* proposant une refonte totale du système d'aménagement des forêts publiques. Ce nouveau régime forestier devrait entrer en vigueur en 2013, en faisant notamment la part belle à l'intensification de la production foresterie sur une portion restreinte du territoire. Parmi les recommandations de la Commission d'étude sur la gestion de la forêt publique québécoise (2004), la culture d'arbres à croissance rapide a été proposée comme une avenue à privilégier pour atténuer les pénuries anticipées de la ressource forestière.

1.2 Objectif général

Cette recherche doctorale s'articule autour de trois objectifs généraux. Le premier objectif (1) est de déterminer les conditions environnementales favorisant l'établissement et la croissance juvénile de peupliers hybrides en plantations sur un site forestier boréal. Le deuxième objectif (2) est d'identifier les techniques d'aménagement sylvicoles (préparation mécanique du sol, contrôle de la compétition végétale, et fertilisation, ainsi que leurs interactions) permettant d'atteindre ces conditions favorables. Le troisième objectif (3) est d'interpréter les processus écologiques soutenant la réponse du peuplier hybride aux conditions induites par l'aménagement sylvicole. Des objectifs spécifiques sont ensuite établis pour chaque chapitre; ils sont décrits à la section 1.5, « Plan de la thèse ».

1.3 Pertinence du projet de recherche

Cette section expose le caractère novateur de la présente recherche doctorale. La pertinence scientifique y est précisée, et le choix du sujet d'étude y est justifié.

1.3.1 Sujet d'étude – le peuplier hybride

Dans plusieurs régions du monde, la principale espèce arborée à croissance rapide appartient au genre *Populus* (Christersson, 2006 ; Pontailler *et al.*, 1999 ; Rodríguez *et al.*, 2010). Largement répandu de par le monde, et naturellement présent dans les zones tempérées de l'hémisphère nord, le genre *Populus* a été cultivé depuis l'Antiquité, notamment pour sa capacité à coloniser les sites perturbés (Zsuffa et al. 1996). Reconnu pour sa production massive de bois, *Populus* est aussi apprécié pour ses qualités propices à la stabilisation des berges, la protection des champs contre le vent et la phytoremédiation des sols contaminés (Zsuffa et al. 1996). L'introduction en Europe de *P. deltoides* au XVIIe siècle a ouvert la voie à une nouvelle étape de la populiculture : l'hybridation. Bien établie en Europe, la culture du genre *Populus* et de ses multiples hybrides s'est exportée un peu partout dans le monde (Heilman, 1999). Aujourd'hui, les principaux pays cultivant le peuplier sont, en ordre croissant, l'Espagne, la Roumanie, l'Italie, la Turquie, la Hongrie, la France (de 100 000 à 250 000 ha), et finalement la Chine (6 millions ha). Par comparaison, le Canada compte très peu de plantations de peupliers, soit 14 300 ha (van Oosten, 2004), mais possède 35 % des superficies de peuplements naturels de *Populus* indigènes de la planète, soit 28,3 millions ha (Volney *et al.*, 2005).

1.3.2 Étude de cas – le peuplier hybride en sol boréal

Les espèces, clones et hybrides de *Populus* sont très exigeants en matière de nutriments, d'eau et de lumière (Barnéoud *et al.*, 1982 ; Mitchell *et al.*, 1999 ; Paré *et al.*, 2001). Comparés à d'autres espèces, leurs besoins en phosphore et en calcium sont particulièrement élevés (Bernier, 1984 ; Paré *et al.*, 2002). Parallèlement à ces exigences, les peupliers sont également très sensibles à la compétition pour les ressources (Stanturf *et al.*, 2001), notamment au niveau des racines (Messier *et al.*, 2009a). Toutefois, à cause de l'intérêt croissant pour ces arbres et de la faible disponibilité des terres, les plantations sont souvent établies sur des sites marginaux et dans des conditions loin d'être idéales pour la nutrition des arbres (Vande Walle *et al.*, 2007), par exemple à de hautes latitudes de l'hémisphère nord, dans la zone boréale (Christersson, 1996 ; Larchevêque *et al.*, 2010). Le biome boréal

représente 11 % des surfaces terrestres de la planète et inclut 29 % des forêts du monde (Weih, 2004). Étant donné cette grande superficie, la probabilité que de nouvelles plantations de peupliers hybrides soient établies dans cette zone est élevée. Par conséquent, il importe de se pencher sur le comportement du peuplier hybride en sol boréal.

Jusqu'à aujourd'hui, la grande majorité des plantations de peupliers hybrides sous les latitudes nordiques, par exemple en Suède (Christersson, 2008, 2010), ou dans la région transitoire entre les prairies et la forêt boréale du centre du Canada (Amichev *et al.*, 2010 ; Block *et al.*, 2009 ; Pinno et Bélanger, 2009 ; Pinno *et al.*, 2009), se retrouve sur des terres agricoles. Seule une minorité de plantations ont été tentées sur des sites forestiers dans l'est du Canada (Bona *et al.*, 2008 ; Coll *et al.*, 2007 ; Guillemette et DesRochers, 2008 ; Sigouin, 2008). Les plantations de peupliers hybrides installées sur ces sites forestiers, par opposition aux terres agricoles, présentent des défis supplémentaires en matière de fertilité du sol et de nutrition des arbres. En effet, les sols forestiers n'ont pas de long historique d'utilisation anthropique et d'apports en fertilisants comme c'est le cas pour les sols agricoles (Vande Walle *et al.*, 2007), et de ce fait, s'avèrent souvent moins fertiles, du moins en zone boréale.

Les sols de la forêt boréale du Bouclier Canadien (ou Précambrien) – communément de type Podzols (Canada Soil Survey Committee, 1992) – sont souvent froids, acides et pauvres en nutriments. Les pratiques sylvicoles d'aménagement des plantations peuvent toutefois améliorer ces propriétés (Örlander *et al.*, 1990), mais peuvent aussi induire de l'hétérogénéité relativement à la répartition spatiale des ressources du sol. Une telle répartition hétérogène des ressources requiert généralement une adaptation de la part de l'arbre en vue d'acquérir les ressources nécessaires à son développement et à sa croissance (Hodge, 2004). Afin de sélectionner les meilleures pratiques sylvicoles et de planifier un aménagement approprié des plantations d'arbres à croissance rapide, il est primordial de connaître l'effet de ces pratiques sur les conditions du sol, ainsi que les réactions des arbres plantés face aux conditions induites par l'aménagement.

Des tests pour la sélection de clones de peuplier hybride adaptés au climat rigoureux et aux sols infertiles de la forêt boréale québécoise ont montré des résultats prometteurs, avec des

taux de survie et de croissance largement supérieurs aux espèces indigènes de cette région et presque aussi élevés que ceux des peupliers hybrides des régions plus au sud (Gagné, 2005, et P. Périnet, communication personnelle). Cela illustre que même dans ces conditions non typiques de la populiculture, de courtes rotations d'environ 20 ans produisant d'importants volumes (estimés à 200-250 m^3/ha) sont possibles. Par comparaison, l'âge d'exploitabilité absolue des peuplements naturels d'une des espèces feuillues les plus courantes en forêt boréale, le peuplier faux-tremble (*Populus tremuloides*), varie de 41 à 88 ans (Pothier et Savard, 1998). Bien que les recherches sur le comportement du peuplier hybride en sol boréal soient plus nombreuses depuis quelques années, elles demeurent insuffisantes, notamment parce que les plantations existantes ont pour l'instant été testées dans un éventail relativement limité de conditions environnementales (incluant les techniques d'aménagement). Notons aussi qu'à ce jour, aucune plantation de peupliers hybrides en sol québécois n'est encore arrivée au terme de sa rotation. Pourtant, l'attrait pour cette espèce croît constamment, tout comme le besoin de connaissances qui lui est associé.

À partir des considérations énumérées ci-dessus, le peuplier hybride s'avère par conséquent un bon sujet d'étude, car il est exigeant en matière de conditions abiotiques (grands besoins en ressources) et biotiques (intolérant à la compétition). Il devrait donc répondre fortement et rapidement aux manipulations de son environnement par le biais des pratiques sylvicoles. Cela permettra d'évaluer l'influence de ces pratiques d'aménagement des plantations sur l'établissement, la survie, le développement et la croissance des arbres. Les vastes plantations expérimentales de peupliers hybrides établies en forêt boréale, dans le sous-domaine de la sapinière à bouleau blanc de l'Ouest, permettent de tester ces questions à une échelle opérationnelle. De plus, la combinaison de sols peu fertiles (forêt boréale) avec une essence exigeante en matière de ressources (peuplier hybride) crée des conditions optimales pour l'obtention de résultats éloquents (car si demande > offre, il devrait y avoir une réponse observable et significative de la part des arbres, particulièrement avec une espèce à croissance rapide) qui contribueront à l'avancement de la recherche scientifique.

1.3.3 Combinaisons de trois techniques d'aménagement sylvicole

La présente recherche doctorale propose d'étudier trois techniques d'aménagement sylvicole des plantations : la préparation mécanique du sol, le contrôle de la compétition végétale, et la fertilisation. Malgré le grand nombre d'études portant sur chacune de ces techniques d'aménagement, beaucoup moins de travaux se sont attardés à leurs interactions au sein d'un même design expérimental (Allen, 1996 ; Burgess *et al.*, 1995 ; South *et al.*, 1995). Ces études portaient cependant toutes sur des espèces de conifères et ont presque toutes été menées dans le climat doux et tempéré du sud-est des États-Unis, à l'exception d'une seule étude en forêt boréale. Par conséquent, il y a présentement un grand manque de connaissances par rapport aux espèces décidues à croissance rapide dans un contexte boréal et leur réponse aux techniques d'aménagement sylvicole. Considérant l'intérêt grandissant pour ce type de plantations et afin d'en assurer le succès, il est impératif de déterminer quels outils sylvicoles permettront de créer des conditions édaphiques et environnementales favorables.

1.3.4 Point de mire de la recherche – les racines

Le développement des racines revêt une grande importance pour l'établissement des semis (Balisky *et al.*, 1995 ; Burdett *et al.*, 1983 ; Grossnickle, 2005 ; Wolken *et al.*, 2010). Les espèces du genre *Populus* sont connues pour investir une large quantité de carbone dans les parties souterraines (Pregitzer et Friend, 1996). Des questions demeurent toutefois quant à la manière et aux conditions reliées à cet investissement (Woolfolk et Friend, 2003). Les acclimatations des plantes à différents niveaux de disponibilité des ressources du sol varient d'une espèce et d'un milieu à l'autre. La plasticité démontrée par les racines peut avoir d'importants impacts sur l'allocation des ressources et la croissance de la plante (Hutchings *et al.*, 2003).

Étant donné leurs besoins élevés en ressources, les espèces et clones de *Populus* sont reconnus pour être particulièrement sensibles à la compétition (Demeritt, 1990 ; Kabba *et al.*, 2007, 2009 ; Stanturf *et al.*, 2001). En tant qu'espèces intolérantes à l'ombre, ils sont le plus

souvent considérés comme sensibles à la compétition aérienne pour la lumière (Messier *et al.*, 1998). Pourtant, en tant qu'espèces pionnières, ils semblent aussi ne pas tolérer la compétition souterraine pour les nutriments et l'espace (Messier *et al.*, 2009a). Depuis une dizaine d'années, les méthodes de contrôle de la compétition utilisées au Québec ciblent principalement la compétition aérienne (Thiffault et Roy, 2011), bien que la compétition souterraine soit souvent considérée comme ayant davantage d'impacts négatifs (Aspinall, 1960 ; Bloor *et al.*, 2008 ; Casper et Jackson, 1997). La présence de racines compétitrices peut en effet s'avérer un obstacle sérieux à l'établissement d'arbres en plantations (Balandier *et al.*, 2007 ; Collet *et al.*, 2006 ; Nambiar et Sands, 1993). Bien que la science a fait des progrès par rapport à cet aspect du développement des arbres, d'aucuns s'entendent pour affirmer que la compréhension des racines demeure embryonnaire en comparaison avec celle des parties aériennes. Les racines de peupliers hybrides étant envisagées comme un facteur déterminant du succès des plantations de cette espèce, elles ont par conséquent reçu davantage d'attention lors de cette recherche.

1.4 État des connaissances

Cette revue de littérature présente les diverses connaissances et théories scientifiques utilisées au cours de cette thèse. Tout au long du texte, des références et exemples particuliers au cas du peuplier hybride seront présentés, parce qu'il constitue notre objet spécifique de recherche.

1.4.1 Aménagement des plantations

Les étapes initiales de l'aménagement des plantations revêtent une importance capitale afin d'assurer l'établissement, la survie et le développement des arbres. Les pratiques sylvicoles couramment mises en œuvre au sein de plantations sont la préparation mécanique du sol, le contrôle de la compétition et la fertilisation. Chacune sera abordée plus en profondeur dans les sections suivantes.

1.4.1.1 Préparation mécanique du sol

Les cas d'insuccès de plantations d'espèces d'arbres à croissance rapide sont souvent attribuables à une mauvaise sélection des pratiques d'aménagement du sol (Evans, 1999), spécifiquement la préparation mécanique du sol (PMS). Les effets de la PMS sur la création de microsites favorables à la plantation sont assez bien connus (Knapp *et al.*, 2008 ; Sutherland et Foreman, 1995). Par exemple, elle rend le sol propice à la mise en terre des plants, réduit la compétition végétale et améliore généralement la croissance des plants (Thiffault *et al.*, 2003). Les effets de la PMS sur le sol sont sensiblement les mêmes partout, mais son utilité ou les besoins qui demandent son utilisation diffèrent. Alors que l'exposition du sol minéral réduit les dommages causés par le charançon du pin en Suède (Petersson et Örlander, 2003), c'est plutôt l'effet de diminution de la compétition végétale qui est importante en Colombie-Britannique (Örlander *et al.*, 1990). On l'utilise pour favoriser la régénération naturelle après coupe (Karlsson *et al.*, 2002) ou avant la plantation, afin de créer de meilleures conditions de germination et d'établissement des semis (Brand et Janus, 1988 ; McMinn, 1982 ; Örlander, 1987 ; Sutton, 1983).

La PMS est particulièrement bénéfique en zone boréale grâce à son effet positif sur la température du sol (Landhäusser, 2009 ; Örlander, 1987 ; Sutton, 1993), qui autrement est trop basse et s'avère souvent un facteur limitant (Dobbs et McMinn, 1977 ; Ritari et Lahde, 1978 ; Sutton, 1993). Une température plus élevée a ensuite des effets positifs sur la croissance de la tige et des racines (Landhäusser *et al.*, 2001 ; Wan *et al.*, 1999). Un des effets de la PMS est d'exposer le sol minéral, et il s'avère que la conductivité thermique (i.e., la transmission de la chaleur en profondeur) est plus grande pour du sol minéral que pour du sol organique (Örlander *et al.*, 1990). Fleming et al. (1994) ont observé une augmentation moyenne de la température du sol de 4 °C sur des sols scalpés (dont l'horizon organique de surface a été enlevé pour exposer le sol minéral sous-jacent) du Nord de la Colombie-Britannique. Une élévation de la température du sol est importante, car, outre l'effet direct sur la croissance des plantes, elle accélère la décomposition de la matière organique (Draper *et al.*, 1985 ; McMinn, 1985), la minéralisation de l'azote (Piatek et Allen, 1999), et favorise les

réactions d'altération des minéraux riches en calcium, magnésium et potassium (Velbel, 1985).

À court terme, toute perturbation du sol a généralement un effet positif sur la croissance des plants à cause de la modification des propriétés hydriques et thermiques du sol et de la réduction de la compétition. L'effet bénéfique de la PMS est observable parfois davantage sur la survie des semis que sur leur croissance (Newsome, 2001), mais l'inverse est aussi possible (Bedford, 2001). La PMS peut améliorer la croissance durant les premières années, mais avoir moins d'effets à plus long terme (Bedford et Sutton, 2000). Fraser et al. (2006) ont démontré que les gains initiaux en croissance de peupliers faux-tremble après scarification du sol n'étaient pas maintenus dix ans plus tard, et que la préparation mécanique avait certains effets négatifs sur la régénération naturelle par drageonnement de cette espèce.

Dans une étude sur des traitements de préparation du sol d'intensités variables, Haeussler et al. (1999) ont observé que la croissance de pins lodgepole (*Pinus contorta*) et d'épinettes blanches (*Picea glauca*) étaient plus fortes dans les traitements les plus intensifs. Néanmoins, pour les pins, la différence était marginale entre ces traitements très intensifs et les traitements d'intensité moyenne. Les auteurs suggéraient que, sur ces sites pauvres, les traitements d'intensité moyenne étaient suffisants pour réduire l'abondance de la végétation compétitrice et ainsi favoriser la croissance des pins. Dans certaines conditions, les traitements de préparation peuvent parfois même s'avérer moins efficaces que l'absence de traitement (Bedford et Sutton, 2000 ; Bedford *et al.*, 2000). Une préparation trop intense peut défavoriser la croissance (Karamanos *et al.*, 2004 ; Sidiras *et al.*, 2001), contribuer au dessèchement du sol et accentuer les dommages dus au gel (Örlander *et al.*, 1990). Néanmoins, Hawkins et Letchford (2001) mettent en garde contre une évaluation hâtive de l'effet des traitements de préparation, puisque durant les dix premières années après la plantation, les effets peuvent fluctuer d'une année à l'autre entre les traitements.

L'impact de la PMS sur la fertilité du sol est variable, améliorant parfois la mobilisation des nutriments du sol (Ross et Malcolm, 1982), mais la réduisant en d'autres occasions (Messier *et al.*, 1995 ; Yildiz *et al.*, 2010), notamment en causant des pertes de matière organique

(Arocena, 2000 ; Gartzia-Bengoetxea *et al.*, 2009). La PMS expose souvent le sol minéral, typiquement plus pauvre en nutriments que les horizons organiques de surface (Gastaldello *et al.*, 2007). Les pratiques de PMS qui déplacent une partie importante de la couche organique ou qui enfouissent cette couche fertile du sol en profondeur (Morris et Lowery, 1988) peuvent causer un lessivage des nutriments (Bock et Van Rees, 2002 ; Burgess *et al.*, 1995 ; Schmidt *et al.*, 1996 ; St. Arnaud, 1995) et conduire à des pertes de productivité (Fox, 2000). Dyck et Skinner (1990) observent des pertes de croissance de 33 % sur des sites où la matière organique et les débris de coupe ont été enlevés dans une plantation de *Pinus radiata* sur un sol marginal. En contrepartie, le mélange des horizons organique et minéral dû à la PMS favorise la mobilisation des nutriments du sol, en agissant sur l'humidité, l'aération et la température du sol (Read et al. 1973, Ross and Malcolm 1988), et favorisant par la même occasion l'activité des microorganismes (Voss-Lagerlund 1976, Palmgren 1984). En effet, Nordborg et al. (2003) ont constaté que les traitements de scarifiage qui préservaient la matière organique offraient les meilleurs taux de minéralisation de l'azote. Néanmoins, Örlander et al. (1996) ont observé des effets bénéfiques à long terme de la PMS sur la croissance de pins sylvestres (*Pinus sylvestris*) plantés sur des sols préparés mécaniquement dont le contenu en carbone et en azote était faible.

Plusieurs études citées ci-dessus soutiennent l'existence d'un réel effet bénéfique à court terme de la PMS sur la fertilité du sol, alors que d'autres constatent des impacts négatifs à courte et longue échéance (MacDonald et al. 1998). Dans des cas extrêmes, cela peut occasionner des pertes par lessivage (MacDonald et al. 1998), lorsque les semis sont incapables d'absorber la totalité des nutriments mobilisés par la PMS (Ross et Malcolm, 1982). Ainsi, Messier et al. (1995) ont observé une perte en fertilité du sol causée par le mélange des horizons; cette préparation du sol a néanmoins entraîné une augmentation en croissance, qui a été attribuée à une réduction de la compétition végétale due à la préparation plutôt qu'à une disponibilité accrue des nutriments. Miller et al. (2006) observent aussi une perte en éléments nutritifs du sol après 15 ans dans des plantations ayant subi diverses préparations de terrain et de contrôle de la végétation. Nordborg et al. (2006) soutiennent qu'on peut conserver la fertilité du sol en enfouissant la matière organique plus profondément sous le sol minéral, ce qui limiterait l'augmentation de la température, et donc des taux de

décomposition, malgré la préparation du sol. Selon les observations de MacKenzie et al. (2005), la préparation de sol favorisait effectivement le développement des plantes, la température et la texture du sol, mais n'aurait aucun effet notable sur la fertilité du sol. Bassiriad (2000) souligne qu'une élévation de la température du sol se traduit par une augmentation de la capacité d'absorption de N et P par les plantes. Il indique aussi que la préférence des racines pour NH_4 par rapport à NO_3 pourrait diminuer avec l'augmentation de la température de la rhizosphère, possiblement dû à une augmentation de la capacité d'absorption du NO_3 par les racines lorsque cette température est supérieure à 14°C. Il suggère par ailleurs que les cinétiques d'absorption de N par les racines pourraient s'avérer un bon indicateur biologique de la capacité de l'écosystème à retenir l'azote (Bassirirad 2000).

Selon les résultats de Nohrtstedt (2000), la préparation mécanique du sol peut avoir un impact positif sur la minéralisation de l'azote. Pour *Picea engelmannii*, les résultats de Grenon et al. (2005) suggèrent que le taux de minéralisation de l'azote (N) dans le sol constitue le meilleur indicateur de l'effet du site sur le développement de la plante. Les sols froids et acides de la forêt boréale présentent souvent de faibles taux de décomposition et de minéralisation de l'azote (i.e., le processus par lequel les microorganismes du sol transforment le N présent sous forme organique dans le sol – une forme largement inaccessible pour les plantes – en NH_4 ou NO_3 – des formes plus disponibles pour absorption par les racines), mais surtout de faibles taux de nitrification (transformation de NH_4 en NO_3), ce qui fait que NH_4 est souvent plus abondant que NO_3 (Lavoie *et al.*, 1992). Woolfolk et Friend (2003) ont établi l'importance de la forme sous laquelle se trouve l'azote dans le sol, soient NH_4^+ ou NO_3^-, pour le développement des racines de *Populus* : le rapport idéal était dans ce cas de 80 % du N sous forme de NO_3^-. Pourtant, dans d'autres études, certains clones ont démontré une préférence pour NH_4 par rapport à NO_3 dans des conditions de pH du sol élevé (pH 7 à 8), ce qui a été attribué à un stress stomatal menant à un déséquilibre ionique interne et une augmentation de l'évapotranspiration, qui résultait de l'acquisition de NO_3 par ces clones de peuplier (Choi *et al.*, 2005 ; DesRochers *et al.*, 2006 ; DesRochers *et al.*, 2007).

La PMS améliore les paramètres physiques du sol par son action d'aération et d'ameublissement (Harrisson *et al.*, 1994 ; Read *et al.*, 1973 ; Ross et Malcolm, 1982). Un sol très dense ou compact présente une porosité réduite pouvant être responsable d'une déficience en oxygène et d'une faible disponibilité en eau. Par le fait même, la température en est généralement diminuée. De plus, une densité élevée du sol est un obstacle à la pénétration des racines et au développement de la plante (Armstrong *et al.*, 1976 ; Örlander *et al.*, 1990 ; Strong et La Roi, 1985). La diffusion de l'oxygène dans le sol est grandement facilitée par des pores remplis d'air plutôt que d'eau (Russel 1977). L'oxygène dans le sol –ou aération– est essentiel à la respiration et à la croissance des racines. L'aération est influencée par la texture du sol. Cette dernière revêt donc une grande importance. Des conditions anoxiques peuvent aussi favoriser la dénitrification et le lessivage de l'azote (Russel 1977). L'aération du sol peut être améliorée par un traitement adéquat de préparation de terrain (Orlander et al. 1990).

La PMS agit sur l'humidité du sol en influençant la texture, la température et le degré de mixité de la matière organique dans le sol (Örlander *et al.*, 1990). Elle permet d'améliorer le drainage du sol en exposant la matière minérale, ce qui favorise une disponibilité accrue de l'eau (Bassman 1989, Pohtila 1977). L'aération d'un sol trop humide peut aussi avoir l'effet de réduire les maladies et la décomposition prématurée affectant les racines (Juzwik and Rugg 1996, Juzwik et al 1997, Sanderson and Armstrong 1978). De plus, l'effet bénéfique de la PMS sur la disponibilité de l'eau pour les arbres plantés provient de son action réductrice sur les espèces compétitrices. Selon Bedford et Sutton (2000), l'effet bénéfique de la PMS est particulièrement visible au sein de sites mal drainés.

Le terme « monticule » est utilisé pour définir une variété de PMS dont la caractéristique principale est de présenter un milieu de plantation surélevé par rapport au sol (Sutton, 1993). La création de monticules préserverait la matière organique du sol tout en améliorant les propriétés physiques et thermiques du sol. Selon Nilsson et Örlander (1999), les monticules augmentent la température du sol (de 10 %) et sont aussi efficaces que l'herbicide pour réduire la compétition. Cependant, Örlander et al. (1990) préviennent que les traitements produisant les températures diurnes et estivales les plus élevées sont aussi ceux qui présentent

les températures nocturnes et hivernales les plus basses (variations journalières et saisonnières), ce qui a été aussi observé par von der Gönna (1989). Les monticules créent de bonnes conditions de drainage, mais il y a possibilité de dessiccation du monticule en période de faibles précipitations si le monticule se trouve par-dessus une couche d'humus inversé, car la couche d'humus empêche alors la migration de l'eau depuis les horizons inférieurs (Örlander *et al.*, 1990).

L'effet de la création de monticules sur la température et l'humidité du sol pourrait varier selon le type de site, soit xérique, mésique ou hydrique (Fryk, 1986). Par exemple, Macadam et al. (2001) recommandent de ne pas utiliser la technique du monticule dans les sites bien drainés ou secs, qui deviendraient alors trop arides. Par ailleurs, Jurgensen (1990) a estimé que la minéralisation de l'azote était dix fois supérieure dans les monticules en comparaison des sites sans PMS. Nohrdstedt (2000) a réfuté l'argument du lessivage du N inorganique dans les monticules, ayant même, au contraire, observé une augmentation de la minéralisation de cet élément. Les travaux de Heineman et al. (1999a) ont démontré que des épinettes plantées en monticules avaient un système racinaire mieux développé qu'en terrain non préparé, ce que Boateng et al. (2009) ont associé plus tard à une croissance et une survie supérieures.

1.4.1.2 Contrôle de la compétition

L'action de la végétation compétitrice a été comparée à une réduction de la disponibilité des ressources (Pearson *et al.*, 1984 ; Perry, 1985). Le contrôle de la compétition est donc essentiel à l'établissement des plantations, afin d'assurer aux arbres un accès adéquat aux ressources en lumière, eau et nutriments (Hansen et Netzer, 1985 ; Schuette et Kaiser, 1996 ; von Althen, 1981). Les effets de ce contrôle sur le développement initial des arbres plantés sont généralement positifs, puisque les premières années sont les plus critiques pour la survie (Harrington, 2006 ; Löf, 2000 ; McDonald *et al.*, 1999 ; Morris *et al.*, 1993 ; Richardson, 1993). L'effet à long terme a cependant fait l'objet de beaucoup moins de recherches. Dans certaines études, l'effet bénéfique qui avait été observé à l'étape de semis n'était plus significatif plus tard, soit après 15 ans (Quicke *et al.*, 1999), alors que selon d'autres études,

l'effet bénéfique du contrôle de la compétition était toujours visible après 10 à 15 ans (Cain, 1999 ; Czapowskyj et Safford, 1993 ; Jylhä et Hytönen, 2006 ; Mason et Milne, 1999 ; Miller *et al.*, 2006 ; Rose *et al.*, 2006).

La méthode qui est peut-être la plus courante et la plus efficace pour contrer la végétation compétitrice est l'herbicide (Zutter *et al.*, 1999). Son utilisation est toutefois interdite en forêt publique au Québec depuis 2001 (Thiffault et Roy, 2011), tandis que son acceptation sociale est ardue en Ontario (Wagner *et al.*, 1998) et que plusieurs pays d'Europe s'orientent dorénavant vers des méthodes alternatives permettant d'éviter l'usage d'herbicides (Willoughby *et al.*, 2009). De bons résultats peuvent aussi être obtenus par le dégagement mécanique. Certains auteurs recommandent de l'effectuer à plusieurs reprises dans la même année (Biring *et al.*, 2004 ; Sigouin, 2008), mais d'autres ont observé une croissance supérieure lorsque le contrôle se limitait à un seul dégagement mécanique par an (Czapowskyj et Safford, 1993). La préparation mécanique du sol s'avère une manière efficace de réduire la compétition végétale, et son effet peut se maintenir durant plusieurs années après la préparation (Messier *et al.*, 1995 ; Pehl et Bailey, 1983 ; Ross et Walstad, 1986). Par exemple, la création de monticules de sol minéral semble réduire efficacement la compétition, tout comme la combinaison de scarifiage et d'application d'herbicide (Bedford et al. 2000).

Étant donné leurs besoins élevés en ressources, les espèces et clones de *Populus* sont reconnus pour être particulièrement sensibles à la compétition (Demeritt, 1990 ; Kabba *et al.*, 2007, 2009 ; Stanturf *et al.*, 2001). En tant qu'espèces intolérantes à l'ombre, ils sont considérés comme sensibles à la compétition aérienne pour la lumière (Messier *et al.*, 1998). En tant qu'espèces pionnières, ils semblent aussi ne pas tolérer la compétition souterraine pour les nutriments et l'espace (Messier *et al.*, 2009a). Le contrôle de la compétition est typiquement bénéfique pour les peupliers hybrides (Stanturf *et al.*, 2001). Cependant, les résultats expérimentaux semblent diverger; certains auteurs suggèrent qu'enlever seulement la végétation aérienne est suffisamment efficace (Czapowskyj et Safford, 1993), tandis que d'autres insistent sur l'importance d'enlever surtout les parties souterraines des plantes compétitrices (Coll *et al.*, 2007).

Pour de nombreuses espèces végétales, la compétition souterraine est souvent plus importante que la compétition aérienne (Aspinall, 1960 ; Bloor *et al.*, 2008 ; Casper et Jackson, 1997). Elle peut s'avérer un obstacle sérieux à l'établissement d'arbres en plantations (Balandier *et al.*, 2007 ; Collet *et al.*, 2006 ; Nambiar et Sands, 1993) ou à la régénération naturelle (Devine et Harrington, 2008 ; Doležal *et al.*, 2006 ; Kueffer *et al.*, 2007), requérant alors des techniques d'aménagement adéquates (Balandier *et al.*, 2006). Par exemple, les racines de graminées réduisent le développement racinaire, la croissance de la tige et la survie de *Populus tremuloides* en abaissant la température du sol, en entrant en concurrence pour les ressources (incluant l'espace) ou en émettant des composés allélopathiques (Landhäusser et Lieffers, 1998 ; Landhäusser *et al.*, 2007). Par conséquent, le développement racinaire initial des arbres est un facteur fondamental du succès de l'établissement de plantations, puisqu'il favorise la survie et la croissance juvénile (Burdett *et al.*, 1983 ; Grossnickle, 2005 ; McCreary et Duryea, 1987). Hibbs et al. (2003) ont observé des rendements élevés de peupliers hybrides plantés sur des sols mal drainés dans l'ouest de l'Oregon, et ont attribué ces rendements au système racinaire profond et bien développé de ces arbres.

1.4.1.3 Fertilisation

Tout comme en agriculture, où elle est courante depuis fort longtemps, la fertilisation est fréquemment utilisée pour combler les besoins nutritifs et maximiser la croissance des arbres (du Toit *et al.*, 2010 ; Mitchell *et al.*, 1999). Elle s'avère généralement très efficace dans les plantations de peupliers hybrides (Brown et van den Driessche, 2002, 2005 ; Guillemette et DesRochers, 2008 ; van den Driessche, 1999), sauf dans des conditions très particulières de contenu en eau du sol trop faible (DesRochers *et al.*, 2006 ; van den Driessche *et al.*, 2003), de compétition trop forte (van den Driessche *et al.*, 2005), ou d'interaction entre le pH du sol et la source d'azote – NH_4-N ou NO_3-N (Choi *et al.*, 2005 ; DesRochers *et al.*, 2006 ; DesRochers *et al.*, 2007). La fertilisation de peupliers hybrides a été le sujet de plusieurs études au Québec (Bona *et al.*, 2008 ; Guillemette et DesRochers, 2008 ; Lteif *et al.*, 2007, 2008, 2010inpress), dans l'ouest du Canada (Brown et van den Driessche, 2002, 2005 ; DesRochers *et al.*, 2006 ; Patterson *et al.*, 2008 ; Patterson *et al.*, 2009 ; van den Driessche,

1999 ; van den Driessche *et al.*, 2005 ; van den Driessche *et al.*, 2008), ainsi qu'aux États-Unis (Coleman *et al.*, 2006 ; Czapowskyj et Safford, 1993 ; McLaughlin *et al.*, 1985 ; McLaughlin *et al.*, 1987 ; Pearson *et al.*, 2010 ; Zalesny *et al.*, 2008 ; Zalesny *et al.*, 2009 ; Zalesny Jr. *et al.*, 2009b ; Zalesny Jr. *et al.*, 2009a).

1.4.1.4 Interactions entre les techniques

Malgré le grand nombre d'études portant sur chacune des techniques d'aménagement présentées ci-dessus, beaucoup moins de travaux se sont attardés à leurs interactions au sein d'un même design expérimental (Allen, 1996 ; Burgess *et al.*, 1995 ; South *et al.*, 1995). Par exemple, une étude incluant les trois techniques a été menée par Nilsson et Allen (2003) dans des plantations de *Pinus taeda* âgées de 18 ans; en matière de croissance, les arbres ont tiré profit de tous les traitements, mais surtout d'une préparation mécanique du sol intensive. Le contrôle de la compétition et la fertilisation interagissaient avec la PMS de telle sorte que leurs effets sur la croissance des pins différaient selon l'intensité de la PMS (Nilsson et Allen, 2003). Des résultats similaires ont été obtenus par Zhao et al. (2009) pour des plantations de *Pinus elliottii* âgées de 26 ans.

Czapowskyj et Safford (1993) ont constaté que le contrôle de la compétition était plus efficace sur des parcelles fertilisées (à la chaux, pour élever le pH) dans une étude impliquant des peupliers hybrides en sol forestier acide. Les auteurs indiquent toutefois que des clones différents plantés dans des conditions distinctes pourraient donner un tout autre résultat. Par opposition, Löf et Welander (2004) n'ont observé qu'un effet négligeable du contrôle de la compétition (par dégagement mécanique) et aucune distinction entre les parcelles fertilisées et non fertilisées. Powers et Reynolds (1999) ont remarqué après dix ans dans des plantations de *Pinus ponderosa* une plus grande efficacité du contrôle de la compétition sur les sites pauvres et secs. Zhang et al (2006) arrivent à la même conclusion après 26 à 36 ans pour la même espèce. Dans le cas de Haeussler et Kabzems (2005), c'est la texture du sol (compaction, humidité) qui influençait le dénouement de la compétition entre *Populus tremuloides* et *Calamagrostis*, ce dernier étant plus dominant sur sols compactés (et vice-versa). En ce qui a trait à l'interaction entre la préparation de terrain et le contrôle de la

compétition, Fu et al. (2007) ont constaté un impact marginal de la préparation de terrain sur la croissance de plusieurs espèces de conifères dans des sites ayant reçu des applications d'herbicide, alors que ces arbres étaient favorablement influencés par la préparation dans les sites sans contrôle de la végétation compétitrice.

Les exemples précédents portent cependant tous sur des espèces de conifères et ont presque tous été menés dans le climat doux et tempéré du sud-est des États-Unis, à l'exception d'une seule étude en forêt boréale. Par conséquent, il y a présentement un grand manque de connaissances par rapport aux espèces décidues à croissance rapide dans un contexte boréal et leur réponse aux techniques d'aménagement sylvicole. Considérant l'intérêt grandissant pour ce type de plantations et afin d'en assurer le succès, il est impératif de déterminer quels outils sylvicoles permettront de créer des conditions édaphiques et environnementales favorables.

1.4.2 Compétition végétale

Les deux théories traitant de la compétition végétale les plus connues et citées sont celles de Philip Grime et David Tilman. Elles ont toutefois fait également l'objet de controverse. Cette section présente les grandes lignes des théories des deux auteurs, leurs divergences, et finalement, quelques tentatives de concilier les deux.

1.4.2.1 Grime

Grime (1977) avait classé les plantes en trois groupes selon leur stratégie d'acquisition des ressources : les plantes « compétitrices (C) », à croissance rapide et provenant de milieu fertile, mais peu perturbé; les plantes « tolérantes au stress (S) », à croissance lente et vivant en milieu peu fertile et peu perturbé; les plantes « rudérales (R) », à croissance rapide et se retrouvant en milieu fertile et perturbé. Grime avait statué que la compétition était la plus intense dans un milieu productif, à cause du plus grand nombre de voisins. La théorie C-S-R s'applique bien aux herbacées de milieu ouvert que Grime étudiait, des plantes qui redéveloppent un système racinaire chaque année et dont l'habitat est caractérisé par des pics

ponctuels de haute disponibilité des ressources suivis de longues périodes de faible disponibilité. Par contre, elle est moins adéquate lorsqu'il est question d'espèces ayant un système racinaire persistant et vivant dans un milieu où la disponibilité des ressources est homogène dans le temps et l'espace (Craine, 2005).

Selon le raisonnement de Grime, au sein d'un site improductif les ressources ne sont pas suffisantes pour permettre à un grand nombre d'individus de se rendre à maturité, et par conséquent les voisins sont physiquement trop éloignés pour entrer véritablement en compétition (Grime, 1973, 1974, 1977). De plus, les conditions environnementales rudes d'un tel site sont beaucoup plus exigeantes envers les plantes que les compétiteurs ne pourront jamais l'être. Par opposition, sur un site productif la croissance supérieure crée davantage d'opportunités d'interactions entre voisins, et donc la compétition – aérienne et souterraine – devient plus importante (Grime, 1979 ; Huston, 1979 ; Keddy, 1989). Sans jamais clairement le mentionner, les premiers travaux de Grime suggéraient déjà les concepts distincts de « l'intensité » et de « l'importance » de la compétition, plus tard explicités par Welden et Slauson (1986) ainsi que Brooker et al. (2005). Par ailleurs, notons que l'expression « productivité d'un site » a typiquement été utilisée comme synonyme de « fertilité du sol », alors que dans les premières publications de Grime la productivité revêtait une signification plus large, étant simplement dérivée de l'observation d'une biomasse aérienne supérieure.

1.4.2.2 Tilman

Parallèlement, David Tilman a développé, à partir de travaux antérieurs sur des écosystèmes aquatiques (Tilman, 1977), une théorie de compétition pour les ressources (Tilman, 1980, 1982) qui a suscité de nombreuses réactions – plus de 1300 citations de ces deux articles, selon Miller et al. (2005). Pour Tilman, la compétition est toujours présente, quelle que soit la productivité du milieu. Cependant, la compétition a lieu pour la ressource qui est limitante à un endroit donné du gradient de productivité (Grubb, 1985 ; Newman, 1973 ; Tilman, 1982, 1985, 1988). Sur un site productif, la compétition s'effectue davantage au niveau des tiges et pour la ressource en lumière, alors qu'à l'autre extrémité du gradient de productivité la

compétition a lieu au niveau des racines pour les ressources du sol (Tilman, 1988). Pour Tilman, la productivité d'un site est donc fonction de la richesse du sol. Par ailleurs, la concentration de la ressource limitante est dénotée par le symbole *R*. La plus faible concentration de cette ressource que peut tolérer une espèce (ou la concentration minimale nécessaire à son développement) est nommée *R**. L'espèce dont le *R** a la plus petite valeur est considérée comme la meilleure compétitrice : elle peut maintenir sa croissance à des niveaux très bas de disponibilité de la ressource et, par le fait même, en réduire la disponibilité pour les autres plantes.

Quelques auteurs ont signalé diverses situations que la théorie de Tilman ne réussit pas à expliquer (Craine, 2005 ; Craine *et al.*, 2005 ; Miller *et al.*, 2005). Certains considèrent de plus que l'utilisation par Tilman de la concentration moyenne d'un nutriment dans la solution du sol n'est pas adéquate (Craine *et al.*, 2005 ; Raynaud et Leadley, 2004), puisque l'absorption par les racines est déterminée par la concentration à la surface de la racine, dont la valeur peut différer de celle de la solution du sol (Craine, 2005). Aussi, les mesures de concentrations de nutriments ont souvent été effectuées sur des échantillons de sol secs, omettant ainsi toute l'importance de l'humidité du sol par rapport à la disponibilité des nutriments (Craine *et al.*, 2005). Les cinétiques de diffusion des éléments dans le sol et de leur absorption par les racines seraient donc plus importantes pour déterminer l'issue de la compétition végétale que les concentrations moyennes des éléments. Chapin et al. (1986) suggèrent pourtant que la capacité d'absorption ne serait importante que pour les ions très mobiles (e.g., K^+ et NO_3^-). La portée d'absorption des racines est supérieure dans le cas de ces ions, et il pourrait donc y avoir superposition des sphères d'influence des racines voisines. Dans cette optique, la compétition pour les ions moins mobiles (e.g., PO_4^{3-}) se ferait par l'élongation du système racinaire, tel que le préconisaient Nye (1977) et Nye et Tinker (1977). Les mycorhizes pourraient aussi jouer un rôle important dans l'acquisition du phosphate (Chapin *et al.*, 1986 ; Hodge *et al.*, 2010 ; Tinker et Nye, 2000), mais aussi de l'azote (Hodge *et al.*, 2010) et de l'eau (Lehto et Zwiazek, 2011 ; Ruth *et al.*, 2011). Grams et Andersen (2007) ont suggéré que les stratégies développées en réponse à la compétition souterraine pouvaient refléter la plasticité physiologique et morphologique du système racinaire des arbres.

1.4.2.3 Confusion et conciliation

Si les théories de la compétition de Grime et Tilman ne tiennent pas compte de la diffusion des nutriments dans le sol (Huston et DeAngelis, 1994 ; Loreau, 1998 ; Raynaud et Leadley, 2004), c'est parce que la première provient d'expérimentations sur des herbacées dans des milieux où la disponibilité des nutriments est hétérogène dans le temps (pic concentré en début de saison), et que l'autre tire son inspiration d'études sur des milieux aquatiques où la distribution des nutriments est uniforme dans l'espace (Craine, 2005). Pourtant, en milieu forestier, les nutriments peuvent être distribués de manière uniforme dans le temps, mais de manière hétérogène dans l'espace, d'où les contradictions avec les théories fondatrices. Notons néanmoins que Paré et al. (1993) et Paré et Bergeron (1995) ont démontré que des épisodes d'épidémies d'insectes pouvaient avoir un effet sur les quantités de nutriments retrouvées dans les sols forestiers.

De plus, les mécanismes sous-jacents à ces théories n'ont jamais été formellement vérifiés, outre dans deux études sur des plantes annuelles de champs (Tilman et Wedin, 1991 ; Wedin et Tilman, 1993). Au cours de ces études, Tilman et son équipe ont observé que l'espèce de première succession, ayant une croissance aérienne (« relative growth rate », RGR) supérieure, mais une allocation aux racines inférieure, était systématiquement supplantée par les espèces de dernière succession, et ce, à tous les niveaux de fertilité (Tilman et Wedin, 1991). La RGR n'était donc pas une bonne représentation de la compétition. La théorie de Tilman prédisait que la compétition se ferait pour la ressource limitante, et donc qu'une espèce de milieu pauvre devrait être un meilleur compétiteur. Pourtant, dans les travaux empiriques de Tilman, ce sont les espèces de milieux riches (fin de succession) qui étaient les meilleures compétitrices pour les ressources du sol. Les espèces de fin de succession étaient néanmoins celles qui abaissaient le plus la concentration moyenne de N dans le sol lorsque cultivées en monocultures (Tilman et Wedin, 1991), ce qui venait appuyer le concept de R^*.

Ces études faisaient appel à des analyses de concentrations moyennes de nutriments effectuées sur des échantillons combinés de sols secs (Tilman et Wedin, 1991), ou des

échantillons frais, mais provenant de sites ayant reçu des apports supplémentaires en eau pour en uniformiser les taux d'humidité (Wedin et Tilman, 1993), ce qui signifie que la diffusion et l'hétérogénéité des nutriments dans le sol n'étaient pas du tout prises en compte, malgré leur importance avérée (Chapin *et al.*, 1986 ; Huston et DeAngelis, 1994). Quelques auteurs ont conçu des modèles incluant la diffusion dans leurs paramètres (Craine *et al.*, 2005 ; Huston et DeAngelis, 1994 ; Loreau, 1998 ; Raynaud et Leadley, 2004) et sont arrivés à des résultats contredisant la théorie de réduction de la concentration moyenne de Tilman. L'exception était lorsque la diffusion était « totale » (i.e., uniforme), signifiant que la théorie de la réduction de la concentration moyenne ne s'appliquerait qu'à un seul extrême du gradient de diffusion (Raynaud et Leadley, 2004).

Dans les écosystèmes terrestres, les propriétés du sol (texture, densité, température, humidité, etc.) pourraient être beaucoup plus importantes que les concentrations moyennes de nutriments pour déterminer l'issue de la compétition chez les plantes, car la diffusion des nutriments serait sensible à la texture et l'humidité du sol (Craine *et al.*, 2005 ; Raynaud et Leadley, 2004 ; Tinker et Nye, 2000). Le modèle analytique de Raynaud et Leadly (Raynaud et Leadley, 2004) suggère que l'expansion du système racinaire (« occupation de l'espace » : nombre de racines par unité de volume de sol) est de première importance en présence d'un faible taux de diffusion, alors que lorsque la diffusion est plus élevée, c'est la « force d'acquisition » (la surface racinaire multipliée par la cinétique d'absorption) qui définit le meilleur compétiteur.

La confusion émane aussi du fait que les deux théories ne s'attardent pas tout à fait au même concept. Alors que Tilman mesure l'intensité de la compétition, Grime évalue plutôt l'importance de la compétition (Brooker *et al.*, 2005 ; Welden et Slauson, 1986). L'intensité est reliée à la physiologie des individus, alors que l'importance regroupe des notions d'écologie et d'évolution s'appliquant à l'échelle des communautés (Welden et Slauson, 1986). Les méthodes d'analyse de la compétition peuvent parfois être biaisées envers l'un ou l'autre de ces concepts, et plus souvent en faveur de l'intensité (Brooker *et al.*, 2005). Selon Ladd et Facelli (Ladd et Facelli, 2007), peu d'études portant sur la compétition ont combiné à la fois des travaux de terrain et des expériences en serre, et que souvent l'utilisation d'une

seule de ces options fait en sorte que les résultats soutiennent davantage une théorie que l'autre.

Pour ajouter à la confusion, on observe que l'importance et l'intensité de la compétition ne sont pas nécessairement corrélées chez certaines espèces végétales (Brooker *et al.*, 2005 ; Reader *et al.*, 1994 ; Welden et Slauson, 1986), alors qu'elles le sont pour d'autres (Brooker *et al.*, 2005 ; Pugnaire et Luque, 2001). Cette divergence pourrait être due à des conditions environnementales particulières (Brooker *et al.*, 2005). La conciliation entre les théories de Grime et de Tilman a été tentée (Craine, 2005 ; Grace, 1991 ; Grubb, 1994), mais demeure encore aujourd'hui matière à polémique (Craine, 2007 ; Grime, 2007a ; Tilman, 2007). Craine (2005) s'étonnait que malgré un grand nombre de recherches menées sur la compétition végétale, très peu d'entre elles (Tilman et Wedin, 1991 ; Wedin et Tilman, 1993) se soient attardées aux mécanismes sous-jacents des théories de la compétition, par exemple en mesurant les concentrations de nutriments dans la solution du sol.

1.4.3 Les racines

Les programmes intensifs de sélection et de reproduction ayant comme objectif d'augmenter la productivité des espèces arborées forestières ont surtout misé sur les traits de la tige plutôt que ceux des racines (Ford, 1976 ; Friend *et al.*, 1999 ; Rae *et al.*, 2004). Selon Friend et al. (1999), ces programmes d'amélioration des arbres devraient mieux utiliser la variabilité génétique des traits des racines tels que la longueur spécifique (i.e., la longueur par unité de poids sec, Eissenstat, 1991), la distribution verticale (Heilman *et al.*, 1994), l'étendue horizontale (Friend *et al.*, 1991), ainsi que la plasticité au niveau de la croissance en réponse à des agrégats de sol riches en nutriments (George *et al.*, 1997 ; Hodge, 2006). Cette dernière pourrait s'avérer particulièrement significative pour le succès de plantations en permettant d'optimiser l'exploration du sol par les racines et d'acquérir efficacement les ressources au sein de sols hétérogènes (Hodge, 2004). Cette proposition revêt une grande pertinence étant donné que l'hétérogénéité spatiale est très répandue dans les écosystèmes naturels (Kohlpaintner *et al.*, 2009 ; Okin *et al.*, 2008 ; Rodríguez *et al.*, 2009). De plus, l'hétérogénéité, à la fois spatiale et temporelle (Kelly, 2008), joue un rôle important dans

l'explication de la coexistence des espèces (Pacala et Tilman, 1994 ; Tilman, 1982 ; Tilman et Pacala, 1993).

1.4.3.1 Allocation des ressources au sein de la plante

L'allocation par la plante de ressources pour la production et l'entretien des racines est souvent comparée à l'allocation vers d'autres parties de la plante, la tige notamment (d'où le populaire ratio tige : racines). Les stratégies d'allocation des ressources ont été formellement rassemblées sous le vocable de la « Théorie de l'allocation optimale » (Bloom *et al.*, 1985), basée sur des principes économiques. Cette théorie soutient que les plantes allouent leurs ressources aux divers organes et fonctions selon l'ordre suivant : respiration > racines fines et feuillage > fleurs et semences > croissance en longueur des branches, de la tige et des racines > croissance en diamètre (Oliver et Larson, 1990 ; Waring et Schlesinger, 1985). Dans le cas des organes d'acquisition des ressources (les feuilles pour la lumière, et les racines pour l'eau et les nutriments du sol), l'allocation dépend aussi de la disponibilité des ressources dans l'environnement. Ainsi, les plantes investissent davantage pour la production des organes d'acquisition dont la ressource associée se trouve en quantité limitée dans leur environnement (Rook, 1991), ce qui est parfois nommé « l'Hypothèse de croissance équilibrée » ("Balanced-Growth Hypothesis", Shipley et Meziane, 2002). Cette hypothèse est cohérente avec les observations de plantes croissant sur sol pauvre dont le système racinaire est plus développé que celui des plantes sur sol riche, et dont l'allocation de ressources aux racines est proportionnellement supérieure à l'allocation à la tige (Keyes et Grier, 1981 ; Reynolds et D'Antonio, 1996 ; Shipley et Meziane, 2002). Aussi, la compétition, en entraînant une diminution de la disponibilité de la ressource qui en est la cause, peut induire une réallocation des ressources entre la tige et les racines.

On retrouve néanmoins certains exemples divergents où une faible disponibilité des ressources ne provoque pas une allocation accrue vers les organes d'acquisition correspondants (Cahill, 2003 ; Gedroc *et al.*, 1996 ; Millett *et al.*, 2008 ; Müller *et al.*, 2000). Selon Müller et al. (2000) et Cahill (2003), des changements observés au niveau de l'allocation aux parties aériennes ou souterraines seraient des stratégies liées au stade de

développement plutôt qu'une véritable réponse plastique aux conditions environnementales. Selon eux, les résultats de Shipley et Meziane (2002) s'expliqueraient donc par le jeune âge des plants, qui permet plus de plasticité (Gedroc *et al.*, 1996), et leur petite taille, qui est naturellement reliée à un ratio tige : racines inférieur (Cahill, 2003), de même que par la distribution homogène des nutriments de leur étude.

1.4.3.2 Plasticité racinaire

La plasticité des racines peut s'exprimer tant au niveau de la morphologie (e.g., le ratio tige : racines) que de la physiologie (e.g., les taux d'absorption ou d'exsudation), mais le processus de plasticité lui-même est encore mal connu (Grams et Andersen, 2007). La croissance racinaire peut être favorisée par la présence de microsites enrichis (Caldwell, 1994), ou encore être déterminée par l'allocation de carbone venant des parties aériennes (Friend *et al.*, 1994). L'azote serait un des principaux éléments déterminant la croissance souterraine des plantes (Friend *et al.*, 1990). Le peuplier répondrait à la disponibilité du N en exhibant une forte plasticité phénotypique de son système racinaire (Friend *et al.*, 1999). De plus, la réponse des racines – et de la tige – à la disponibilité de l'azote dans le sol ne serait pas linéaire, ce qui représenterait un compromis dans les stratégies d'allocation des ressources entre les parties aériennes et souterraines en réaction à une disponibilité variable de l'azote (Kern *et al.*, 2004).

La plasticité revêt une importance capitale pour l'acquisition des ressources par les plantes (De Kroon *et al.*, 2009 ; Grime, 1994 ; Grime et Mackey, 2002). Les caractéristiques morphologiques des racines peuvent être modifiées par les arbres, soit au niveau de la racine individuelle ou à celui de tout le système racinaire (Leuschner *et al.*, 2004). Le taux de prolifération en longueur des racines peut augmenter substantiellement lors de l'entrée en contact avec un agrégat de sol où la disponibilité des ressources est élevée (Pregitzer, 2008). La production de racines plus fines avec une plus grande surface racinaire spécifique (SRS, superficie par unité de masse) augmente la surface de tout le système racinaire pour un même investissement en carbone, améliorant ainsi le rapport coût/bénéfice de la production racinaire. Une telle plasticité de la SRS peut aussi améliorer l'acquisition d'eau et de

nutriments par unité de masse de racines, pour un taux d'acquisition par surface constant (Tyree *et al.*, 1998). L'architecture racinaire peut démontrer une grande plasticité en réponse aux conditions de sol, particulièrement la disponibilité des nutriments (Drew *et al.*, 1973 ; Fitter *et al.*, 1991 ; Grime *et al.*, 1986). Hutchings et al. (2003) ont confirmé dans une revue de la littérature qu'une haute densité de racines au sein d'agrégats de sol riches en nutriments avait été observée autant dans des expériences en laboratoire que sur le terrain. Néanmoins, comme il a été suggéré par des études antérieures (Passioura et Wetselaar, 1972 ; Wetselaar *et al.*, 1972) et confirmé plus tard par une revue de littérature (Robinson, 1994), la prolifération racinaire accrue au sein de riches agrégats de sol est loin d'être universellement répandue parmi les espèces végétales, puisque le tiers des espèces revues par Robinson (1994) ne montrait pas de réponse aux riches agrégats.

Par ailleurs, tel que mentionné précédemment (section 1.4.2.2), les mycorhizes pourraient aussi jouer un rôle important dans l'acquisition du phosphate (Chapin *et al.*, 1986 ; Hodge *et al.*, 2010 ; Tinker et Nye, 2000), mais aussi de l'azote (Hodge *et al.*, 2010) et de l'eau (Lehto et Zwiazek, 2011 ; Ruth *et al.*, 2011).

1.4.3.3 Plasticité racinaire et hétérogénéité des ressources

Une perturbation du sol, comme celle induite par la préparation mécanique, peut modifier la distribution spatiale des nutriments, par exemple en créant des agrégats de sol riches en nutriments. La croissance racinaire peut répondre à la présence de ces agrégats enrichis en démontrant une certaine plasticité (George *et al.*, 1997 ; Hodge, 2006). De nombreuses études se sont attardées à la plasticité racinaire en réponse à la distribution spatiale de l'azote chez des espèces de plantes herbacées utilisées en agriculture. Par contre, beaucoup moins de recherches ont ciblé des espèces arborées (Hawkins et Metcalfe, 2008). Une étude notable a été menée par Heineman et al. (Heineman *et al.*, 1999a) au sujet d'épinettes blanches (*Picea glauca*) plantées sur monticule. Ces auteurs ont évalué le sol et les racines le long du profil vertical de sol. Ils ont établi les délimitations verticales de leur échantillonnage selon des intervalles réguliers de profondeur, plutôt que sur le type d'horizon ou de matériau de sol, comme recommandé par Strong et La Roi (1988). De ce fait, leurs résultats ne peuvent pas

vraiment être utilisés pour distinguer les stratégies d'exploration optimale des racines, ou autrement dit la préférence des racines pour un certain type de matériau de sol où proliférer. Selon Hutchings et John (2004), la réponse des plantes à l'hétérogénéité environnementale ne peut pas toujours être prédite par les patrons observés sous des conditions homogènes. Pourtant, cette réponse peut avoir d'importants impacts sur l'allocation des ressources et la croissance de la plante. Les racines ont à leur disposition un éventail de stratégies pour l'acquisition des nutriments au sein d'un environnement hétérogène (Hodge, 2009 ; Hodge *et al.*, 2009). De plus, divers traits liés à l'exploration du sol par les racines sont représentatifs de la réponse à l'hétérogénéité (Rajaniemi, 2007 ; Zhang *et al.*, 2010). Des conditions hétérogènes de sol peuvent induire une réponse plastique en matière de distribution et d'architecture des racines (Bauhus et Messier, 1999b ; Campbell *et al.*, 2002 ; Casper *et al.*, 2003), d'allocation de biomasse entre les parties aériennes et souterraines, et par rapport au rendement total de la plante (Hutchings *et al.*, 2003).

Certaines théories courantes en écologie animale pourraient être appliquées à l'étude des plantes. Ainsi, la théorie de la distribution libre (Fretwell, 1972 ; Fretwell et Lucas, 1970) suggèrerait que les racines se distribuent dans le sol proportionnellement à la quantité de ressources présentes. Par opposition, la stratégie optimale de recherche de la nourriture (MacArthur et Pianka, 1966 ; McNickle *et al.*, 2009 ; Stephens et Krebs, 1986) proposerait plutôt que les racines se distribuent de manière à optimiser le compromis entre la dépense énergétique requise pour accéder aux ressources et la valeur de ces ressources.

1.4.3.4 Plasticité racinaire et compétition végétale

Les racines de certaines espèces végétales ont tendance à proliférer en réponse à la compétition souterraine. Bartelheimer et al. (2006) nomment « stratégie d'agrégation » cette situation où les plantes produisent davantage de racines en présence de compétition et, surtout, carrément dans la zone où se trouvent les racines du compétiteur. Le meilleur compétiteur dont les racines prolifèrent en premier dans un agrégat de sol riche pourrait bien acquérir tous les éléments nutritifs disponibles avant qu'un compétiteur plus faible n'en ait la chance, comme dans la théorie de « l'acquisition hâtive de la réserve » (supply pre-emption,

Barley, 1970 ; Comerford *et al.*, 1994 ; Craine *et al.*, 2005). À l'opposé, Schenk (1999) a montré que les racines de certaines espèces peuvent dans certaines conditions se montrer « territoriales » et demeurer dans les zones de sol où aucun compétiteur n'est présent, ce qu'il a appelé la « ségrégation spatiale ». Les réponses plastiques des racines aux microsites de sol riches en nutriments figurent parmi les facteurs causant la ségrégation. Ces questions de ségrégation racinaire s'avèrent très semblables aux discussions sur les patrons « d'évitement de la compétition » (Messier *et al.*, 2009a). Day et al. (2003b) ont démontré que le patron spatial de distribution des nutriments du sol pouvait altérer le niveau de compétition au sein d'une communauté végétale, avec des impacts sur la croissance et la survie des plantes, ainsi que sur la structure de la communauté.

1.4.3.5 Compétition végétale et hétérogénéité des ressources

Pour une même quantité de nutriments, la compétition pourrait être plus forte au sein de sols présentant des agrégats riches en nutriments par rapport à d'autres sols où la distribution des nutriments est plus homogène (Hutchings *et al.*, 2003). Par conséquent, les patrons de distribution et de disponibilité des nutriments pourraient influencer les interactions inter- et intraspécifique chez les plantes. Caldwell et al. (1996) ont d'ailleurs observé de fortes interactions entre les espèces au sein d'agrégats de sol riches en nutriments. La plasticité racinaire pourrait conférer une forte habileté compétitive dans les environnements hétérogènes (Craine, 2006 ; Fransen *et al.*, 2001 ; Hodge *et al.*, 1999). Par exemple, plusieurs études ont décrit l'avantage compétitif découlant d'une plasticité de la production de racines latérales (De Kroon et Mommer, 2006 ; Hodge, 2006 ; Kembel et Cahill, 2005 ; Kembel *et al.*, 2008).

1.5 Plan de la thèse

Les objectifs généraux de la thèse ont été présentés à la section 1.2. La thèse est ensuite divisée en trois chapitres, qui répondent chacun à une partie des objectifs généraux. Le Tableau 1.1 résume les objectifs spécifiques de chaque chapitre, présente les principaux thèmes qui y sont abordés, et associe les objectifs généraux aux chapitres qui y répondent.

Le chapitre I a comme objectif spécifique d'évaluer sur le terrain la réponse du peuplier hybride aux techniques d'aménagement sylvicoles : préparation mécanique du sol (PMS), contrôle de la compétition végétale, et fertilisation, ainsi que leurs interactions. L'hypothèse à l'essai est qu'un aménagement sylvicole adéquat permet de créer des microsites favorables à l'établissement, la survie et la croissance des arbres.

L'objectif spécifique du chapitre II est d'évaluer sur le terrain le développement racinaire du peuplier hybride en réponse à l'arrangement vertical des horizons de sol induit par la PMS, la dynamique de l'azote, et la présence de racines compétitives. Les théories examinées dans ce chapitre concernent *i*) l'évitement de la compétition, *ii*) la prolifération des racines dans les zones de sol fertiles (i.e., la plasticité), et *iii*) l'amélioration de la minéralisation de l'azote par la PMS.

Le chapitre III a comme objectif spécifique d'évaluer lors d'une expérience en pots la réponse des racines du peuplier hybride à la compétition et la distribution spatiale des nutriments du sol. Les théories suivantes y sont testées : *i*) l'évitement de la compétition, *ii*) la prolifération des racines dans les zones de sol fertiles (i.e., la plasticité), *iii*) le compromis entre les deux précédents comportements, et *iv*) l'avantage d'une distribution hétérogène des nutriments pour la croissance totale de l'arbre.

Tableau 1.1 Résumé des objectifs couverts et des thèmes abordés par chapitre de la thèse.

Chapitre	Objectif spécifique	Objectifs généraux couverts par le chapitre (voir section 1.2)	Thèmes abordés
I	Évaluer sur le terrain la réponse du PEH aux techniques d'aménagement sylvicoles : préparation mécanique du sol (PMS), contrôle de la compétition végétale, et fertilisation, ainsi que leurs interactions.	1 et 2	1) Un aménagement sylvicole adéquat permet de créer des microsites favorables à l'établissement, la survie et la croissance des arbres.
II	Évaluer sur le terrain le développement racinaire du PEH en réponse à l'arrangement vertical des horizons de sol induit par la PMS, la dynamique de l'azote, et la présence de racines compétitives.	2 et 3	1) Évitement de la compétition; 2) Prolifération des racines dans les zones de sol fertiles (i.e., plasticité); 3) Amélioration de la minéralisation de l'azote par la PMS.
III	Évaluer lors d'une expérience en pots la réponse des racines du PEH à la compétition et la distribution spatiale des nutriments du sol.	3	1) Évitement de la compétition; 2) Prolifération des racines dans les zones de sol fertiles (i.e., plasticité); 3) Compromis entre les deux précédents comportements; 4) Avantage d'une distribution hétérogène des nutriments pour la croissance totale de l'arbre.

CHAPITRE I

JUVENILE GROWTH OF HYBRID POPLARS ON ACIDIC BOREAL SOIL DETERMINED BY ENVIRONMENTAL EFFECTS OF SOIL PREPARATION, VEGETATION CONTROL, AND FERTILIZATION

2.1 Abstract

The silviculture of hybrid poplars and other fast-growing tree species is a promising solution to reduce the pressure on natural forests while maintaining wood supplies to industries. However, hybrid poplars are very sensitive to competing vegetation and to inadequate soil conditions and fertility. Possible management tools include mechanical site preparation (MSP), vegetation control (VC), and fertilization. Experimental plantations of hybrid poplars (one clone, *Populus balsamifera* x *P. maximowiczii*) were established at eight formerly forested sites on acidic soil in the southern boreal forest of Quebec, Canada. The objective was to test the response of hybrid poplars to the interaction of several silvicultural tools, which has been rarely done. Four MSP treatments (in decreasing order of intensity: mounding, harrowing, heavy disk trenching, light disk trenching) and a control (unprepared) were all combined with four different frequencies of plant competition control by brushing (from never up to once a year). Fertilization with N or N+P was also tested in three selected MSP treatments. After five years, hybrid poplar tree growth among MSP treatments increased in the following order: unprepared < light disk trenching < heavy disk trenching < harrowing < mounding. MSP was also essential in favouring early tree survival, as illustrated by mortality rates of over 20% in unprepared plots and below 5% in all other MSP treatments. The effect of competition control on hybrid poplar growth was greatest in the less intensive MSP treatments, where competing vegetation was the most abundant. On the contrary, fertilization effect was significant only in the most intensive MSP (mounding). Moreover, neither fertilization nor VC could compensate for inadequate soil preparation. Of all the silvicultural treatments tested, mounding provided the best tree growth despite a nitrogen and carbon impoverished surface soil.

Keywords: hybrid poplar, intensive silviculture, mechanical soil preparation, plant competition, fertilization.

2.2 Introduction

The use of fast-growing plantations on a small proportion of the landscape is a promising silvicultural solution for reducing the pressure on natural forests (Paquette et Messier, 2010). In the context of the forest zoning management approach (Messier et Kneeshaw, 1999 ; Messier *et al.*, 2009b ; Seymour et Hunter, 1992), it has the potential of expanding protected areas and areas under ecosystem management (Başkent et Yolasığmaz, 2003), while maintaining or even increasing wood supply (Binkley, 1997 ; Fox, 2000 ; Messier *et al.*, 2003). In several areas of the world, the fast-growing tree species of choice belong to the genus *Populus* (Christersson, 2006 ; Pontailler *et al.*, 1999 ; Rodríguez *et al.*, 2010). *Populus* trees, clones and hybrids are very demanding in terms of nutrients, water and light (Barnéoud *et al.*, 1982 ; Mitchell *et al.*, 1999 ; Paré *et al.*, 2001). However, because of the increasing interest in using these trees and the low availability of land, plantations are being established on marginal sites and in less than ideal conditions (Vande Walle et al., 2007), for instance at high latitudes of the northern hemisphere, i.e., in the boreal zone (Christersson, 1996 ; Larchevêque *et al.*, 2010). This important biome represents 11% of the Earth's terrestrial areas and includes 29% of the world's forests (Weih, 2004).

To date, hybrid poplar plantations in northern latitudes, for example in Sweden (Christersson, 2008, 2010) or in the prairie–boreal forest transition region of central Canada (Amichev *et al.*, 2010 ; Block *et al.*, 2009 ; Pinno et Bélanger, 2009 ; Pinno *et al.*, 2009), are all located on agricultural lands; only a few have been tested on recently logged or otherwise formerly forested sites of eastern Canada (Bona *et al.*, 2008 ; Coll *et al.*, 2007 ; Guillemette et DesRochers, 2008 ; Sigouin, 2008). Hybrid poplar plantations established at these sites, as opposed to agricultural lands, pose further challenges in terms of soil fertility and tree nutrition since forest soils do not have long histories of anthropogenic use and fertilizer amendments the way agricultural soils do (Vande Walle et al., 2007) and as such are often less fertile, at least in the boreal zone. Selective tests of hybrid poplar clones adapted to the nutrient-poor, acidic soils and relatively rigorous climate of the boreal forest have given encouraging results (Gagné, 2005, and P. Périnet, personal communication). It seems that even in such harsh conditions for poplar plantations, short rotations (< 20 years) producing

large wood volumes are possible. In comparison, the typical rotation for natural stands of trembling aspen (*Populus tremuloides*) is 41-88 years (Pothier et Savard, 1998).

Unsuccessful plantations of fast-growing trees have often been attributed to the selection of inappropriate soil management techniques (Evans, 1999). Mechanical soil preparation (MSP) can produce microsites that are appropriate for tree planting (Knapp *et al.*, 2008 ; Sutherland et Foreman, 1995), while reducing competing vegetation and generally improving tree growth (Thiffault et al., 2003). In boreal zones, it is particularly beneficial for increasing soil temperature (Landhäusser, 2009 ; Örlander, 1987 ; Sutton, 1993), which in turn increases leaf, shoot and root growth (Landhäusser *et al.*, 2001 ; Wan *et al.*, 1999). The impact of MSP on soil fertility is more variable, sometimes improving nutrient mobilization (Ross et Malcolm, 1982) and on other occasions reducing it (Messier *et al.*, 1995 ; Yildiz *et al.*, 2010), notably due to soil organic matter removal (Arocena, 2000 ; Gartzia-Bengoetxea *et al.*, 2009). Given that hybrid poplars have high needs for resources, they are also known to be particularly sensitive to competition (Kabba *et al.*, 2007, 2009 ; Stanturf *et al.*, 2001). Competition control generally has positive effects on early development of seedlings because the first few years are the most critical for survival (Harrington, 2006 ; Löf, 2000 ; Morris *et al.*, 1993). The control of competing vegetation typically proves beneficial to hybrid poplars (Stanturf et al., 2001), although experimental results may diverge, with some pointing towards effectiveness of the removal of aboveground vegetation only (Czapowskyj et Safford, 1993) while others insist on the need to target belowground plant parts (Coll et al., 2007). Fertilization is also frequently used to fulfill nutritional needs and to maximize tree growth (du Toit *et al.*, 2010 ; Mitchell *et al.*, 1999). It is generally very effective in poplar plantations (Brown et van den Driessche, 2002, 2005 ; Guillemette et DesRochers, 2008) and has been extensively studied (Coleman *et al.*, 2006 ; Guillemette et DesRochers, 2008 ; Lteif *et al.*, 2008 ; Patterson *et al.*, 2009 ; Pearson *et al.*, 2010).

Although the aforementioned management tools, i.e., MSP, vegetation control (VC), and fertilization, have been the object of several studies, very few have combined the three of them in a single design looking at multiple interactions (Allen, 1996 ; Burgess *et al.*, 1995 ; South *et al.*, 1995). One example of a three-factor study comes from Nilsson and Allen

(2003) and was conducted in 18-year-old loblolly pine (*Pinus taeda* L.) plantations. Tree growth benefited greatly from all treatments, but mostly from high intensity MSP. Fertilization and VC interacted with MSP so that their effects on pine growth differed depending on MSP intensity (Nilsson et Allen, 2003). Similar results were obtained in a recent study by Zhao et al. (2009) on 26-year-old stands of slash pine (*Pinus elliottii* Engelm.).

The preceding examples were all concerned with coniferous trees and were mostly conducted in the mild, temperate climate of southeastern USA, with only one being conducted in the boreal forest. Consequently, studies focusing on deciduous fast-growing trees in a boreal context and looking at several silvicultural techniques are currently lacking, which does not bode well considering the growing interest in intensive silviculture in the boreal forest. To ensure the success of these plantations, it is thus imperative to assess which silvicultural tools will provide favourable soil and environmental conditions. The main objective of this unique study was to test the interactions of various MSP techniques, VC frequencies and fertilizer applications within industrial-scale experimental plantations of hybrid poplars established on former boreal forest sites with cold, nutrient-poor, and acidic soils of the Precambrian Shield.

2.3 Methods

2.3.1 Sites

Eight formerly forested sites were chosen in the Saguenay–Lac-Saint-Jean region (between 48°08' and 48°43' N, and between 71°05' and 72°52' W) of the province of Quebec, Canada. These sites are located in the southern boreal forest, and original stands consisted of balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), and paper birch (*Betula papyrifera*); more stand data are shown in Appendix. Soils are representative of Precambrian Shield settings characterized by coarse acidic soils, and are classified as Orthic ferro-humic Podzols (Canada Soil Survey Committee, 1992) or Haplorthods (Soil Survey Staff, 1998). Mean annual temperature for this region is 2.2°C and mean annual precipitation is 1000 mm (of which 710 mm is rainfall),

while mean summer (June-September) temperature is 15.5°C and mean summer monthly precipitation (rainfall) is 107.5 mm (Environment Canada, 2009).

2.3.2 Mechanical Soil Preparation (MSP)

Sites were whole-tree harvested in summer 2002; then, soils were mechanically prepared in fall 2003 after the regenerating vegetation had been cleared with a brush saw in late summer. Five techniques were tested, which represent an increasing gradient of soil disturbance intensity at the tree or microsite level: no preparation (control), light disk trenching, heavy disk trenching, harrowing, and mounding. In control plots, no soil preparation was done after harvest and trees were planted directly wherever it was possible to do so. Light disk trenching was done with a TTS Delta disk trencher that involved two hydraulically-driven rotating dented disks that were ran in parallel straight rows to remove the surface organic layer (up to 20 cm deep) and expose the mineral soil in which trees were planted. Heavy disk trenching used the same machinery, but three runs of the machinery were done, with the first two runs perpendicular to each other and the last one diagonal to these. Harrowing followed the same three-run pattern, but the equipment involved three rows of five 75-cm diameter disks pulled by a tractor. These disks are larger and can dig much deeper into the soil than those of the disk trencher. The disks were slightly inclined at an angle that varied between disks and rows to ensure that the soil (both the mineral and organic layers) was thoroughly mixed. Mounding is a common treatment in Scandinavia and Canada (Örlander *et al.*, 1990 ; Sutton, 1993), and here it was done using a mechanical shovel equipped with a 45-cm-wide bucket that dug deep into the soil through the surface organic layer in order to retrieve mineral soil. This mineral soil was then upturned over undisturbed soil to form a mound about 30 cm in height and 50 cm in radius. In this manner, it buried the original organic soil material and crushed the vegetation beneath it. Trees were planted directly in, but slightly on the side of the mound, and given the height of the mound the lower end of a tree barely reached the organic layer. Each of these five treatments covered a 1-ha plot and was repeated at each of the eight sites (its placement relative to other treatments was randomized), hence $n = 8$ over a total of 40 ha of plantations (Fig. 2.1).

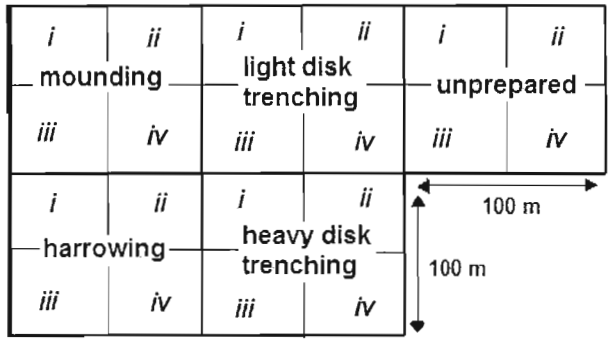

Figure 2.1 Example site (n = 8) of treatment plots in the experimental hybrid poplar plantations. Each of the four mechanical soil preparation (MSP) treatments and the control covers 1 ha, and treatments are randomized within a site. The four vegetation control (VC) subplots (randomized within each MSP plot) are: *i*) never, *ii*) once a year at year 2, *iii*) once a year at years 1 and 3, and *iv*) once a year at years 1, 2 and 3.

2.3.3 Tree planting

Bare-root, ~ 1-m-tall hybrid poplar tree cuttings of the 915319 clone *Populus maximowiczii* x *Populus balsamifera* (Périnet et al., 2001) were obtained from a nursery operated by the Ministère des Ressources naturelles et de la Faune du Québec at Grande-Piles, QC, Canada. The cuttings were produced in the spring from parent trees in the nursery plantations, and cultivated over the summer in irrigated, fertilized, and weeded soil. This allowed them to develop a substantial root system, which was subsequently groomed in the fall when the cuttings were dormant, a state in which they were kept until shipping to the field the next spring. The bare-root cuttings were hand-planted with a shovel in April 2004 at a depth of 20-30 cm and in straight rows at a spacing of 3 x 3 m (density = 1100 trees ha^{-1}). Throughout this text, the year of planting will be considered as year 1.

2.3.4 Vegetation Control (VC)

Competing herbaceous and woody plants were mechanically removed by brushing (aboveground parts only), during or after the peak of summer biomass production (mid-July to beginning of August). The four VC treatments corresponded to four different frequencies: *i*) never, *ii*) at year 3, *iii*) at years 2 and 4, and *iv*) at years 2, 3, and 4. These treatments were

tested using four 0.25-ha (50 m x 50 m) subplots that were delineated and placed randomly within each 1-ha MSP plot (Fig. 1), for a total of 160 subplots. Three of these subplots were not used in further analyses because of misallocated treatments, leaving 157 subplots. In this text, plots that were never controlled for competition will be commonly referred to as "unweeded", in contrast to the other VC plots that will be called "weeded".

2.3.5 Fertilization

In July of year 5, two doses (0 as control and 400 g $tree^{-1}$) of fertilizers (N only, as 18-0-0; and N+P, as 18-46-0) were applied at the base of selected trees. Each fertilizer treatment was replicated on five trees chosen randomly in the VC subplot *iii* of two MSP treatments (harrowing and mounding) and the control (unprepared) across all eight sites. Care was taken not to choose adjacent trees, thus they were separated by at least one tree row (i.e., 6 m apart). These trees were located in the buffer zone of the 0.25-ha plots (see section 2.6), so as not to fertilize any tagged trees.

2.3.6 Growth surveys

Total height, diameter, and annual shoot lengths were measured on 12 trees in each 0.25-ha subplot (see 2.4) in October of years 3 and 5. These 12 tagged trees were chosen randomly within a 20 x 20 m area in the center of the subplot, leaving a 15-m strip on all sides where no trees were tagged for measurements. This 15-m strip was called the buffer zone. The subset of fertilized and unfertilized trees (located in the buffer zone) was measured in October of years 5 and 6.

2.3.7 Assessment of competition cover

In 2005, interspecific competition was assessed for six trees chosen randomly among the 12 surveyed trees per 0.25-ha subplot at all the sites in the two VC subplots that did not undergo brushing that year, hence treatments *i* and *ii*. These treatments had never been weeded between site preparation, tree planting and competition surveying. Within a 1-m radius

divided in four quadrats around a hybrid poplar tree, the percentage of the area covered by competition was visually evaluated and classified by plant type as tree, shrub, herbaceous or grass. This was done separately for each quadrat and subsequently averaged for the whole tree.

2.3.8 Foliar analyses

Leaves were sampled every year from year 3 to 5. In year 3, one leaf from each of the 12 surveyed trees per 0.25-ha subplot was pooled (157 samples). In year 4, leaves were sampled at all sites in August in all four MSP treatments and the control and in two VC treatments, *i*) never and *iv*) years 2-3-4. All 12 surveyed trees were individually sampled in each subplot, and five leaves were taken from each tree at regular intervals along the vertical length of the crown. In year 5, sampling was repeated similarly to the previous year, but only in the VC subplot *iv*. Fertilized trees were sampled in August of years 5 and 6, and leaves from trees in a same plot were pooled by treatment (unfertilized, N-fertilized, N+P-fertilized). Foliar samples from all years were oven-dried at 70°C for 48 h. Total N was determined as for the soil samples on a LECO CNS analyzer (LECO Corporation, St. Joseph, MI, USA), while phosphorus was determined following calcination at 500°C and dilution with hydrochloric acid (Miller, 1998). Phosphorus was analyzed by flow injection analysis and ion chromatography (FIA; Lachat Instruments, Milwaukee, WI, USA), and base cations by atomic absorption and emission (Varian, model AA240FS, Palo Alto, CA, USA).

2.3.9 Soil analyses

2.3.9.1 General characteristics

In year 2, one mineral soil sample was taken, in the center of each 0.25-ha subplot, at a depth of approximately 15-20 cm, thus reaching into the B-horizon. These mineral soil samples (n = 157) served to describe the plots and sites in a general way and ensure that heterogeneity had been reduced to a minimum when initially choosing sites prior to mechanical soil preparation. These descriptive soil data were thus not used in explaining tree growth

responses to the various treatments. Soil pH was analyzed in distilled water and $CaCl_2$ (Hendershot et al., 2007). Exchangeable cations (K, Ca, Mg, Al and Fe) were extracted using unbuffered 0.1 M $BaCl_2$ and determined by atomic absorption and emission (Hendershot et al., 2007). Soil particle size distribution (texture) was determined by the hydrometer method (Gregorich et Beare, 2007) without pre-treatment of the samples due to the low organic matter content, coarse nature of the particles and low level of aggregation of the samples.

In year 4, one soil pit was dug in the VC subplot *iv* of every 1-ha MSP plot (n = 40) to characterize vertical soil profiles; horizons were identified and their thickness measured, while a sample was taken from the B-horizon with a cylinder of known volume to later calculate B-horizon bulk density. This sampling served in describing the sites and not in explaining tree growth responses. Site means of the general soil characteristics are presented in Table 2.1.

Table 2.1 General soil characteristics of the mineral B-horizon (sampled at a depth of 15-20 cm). Values are means for eight sites, with standard deviation.

Soil variable	Site mean	SD
Texture		
Clay, %	5.0	1.2
Silt, %	24.7	4.9
Sand, %	70.3	4.8
CEC, $cmol_c\ kg^{-1}$	2.27	2.4
pH	4.13	0.17
BS, %	53.3	16.1
Bulk density, $g\ cm^{-3}$	1.05	0.16

2.3.9.2 Physico-chemical characteristics

Soil penetrability, humidity, and temperature were assessed during year 4, and were subsequently compared to tree growth in trying to explain responses to the various treatments.

In June of year 4, soil penetrability was evaluated at the base of each of the 12 surveyed trees in the harrow and mounding MSP treatments and the unprepared control (288 trees) with a

drop-hammer penetrometer (model PEM-1 from Roctest Ltd., Saint-Lambert, QC, Canada), where a weight of 4.5 kg was dropped repeatedly from a height of 46 cm to drive a metal rod into the ground; the depth reached by the rod after 10 hits represented soil penetrability. Since rocks can hamper the efficiency of this method, several trials were done around a tree to ensure adequate representation of soil conditions.

In August of year 4, soil volumetric water content was measured with a TDR-300 soil moisture meter equipped with two 20-cm probes (Spectrum Technologies Inc., Plainfield, IL, USA). A mean value per tree was obtained from four measurements taken around the base of each of the 12 surveyed trees in the harrow and mounding MSP treatments and the control at all sites (288 trees). Repeatability of water content measurements was verified by sampling twice at seven 0.25-ha subplots found across three sites, either before and after a rainy day or over a period of 2 weeks in August of year 4; results of matched-pairs *t*-tests showed these measurements to be satisfyingly similar despite the different conditions in which they were taken.

Soil temperature was measured at the base of each tree with a hand-held, 20-cm electronic thermometer probe. Measurements were taken across all sites between June and August of year 4, and were repeated 2-3 times over the season for each tree, approximately once per month. By doing so, temperature measurements were satisfyingly consistent for individual trees. Data-logging temperature sensors (Maxim Integrated Products, Sunnyvale, CA, USA) were also placed at two sites in two VC subplots (*i* and *iv*) of all four MSP treatments and the control. Soil temperature was measured every 2 h from the beginning of June to the end of October of year 4, at depths of 2, 10 and 20 cm. The sensors' data were compared with the hand-held thermometer probe measurements to further verify data reliability.

2.3.9.3 N mineralization rates

Tree growth responses to treatments were additionally submitted to the comparison with soil nutrients data, namely the mineralization of N.

Potential N mineralization was assessed by comparing nitrate (NO_3) and ammonium (NH_4) concentrations at the start and at the end of a 6-week (from the beginning of July to mid-August of year 4) closed-top *in situ* incubation with 30-cm-long PVC tubes as described in Brais et al. (2002a). Tubes were inserted in the surface soil (0-20 cm) at a distance of 30 cm from the base of three trees per 0.25-ha subplot in two MSP treatments (harrowing and mounding) and the control, and within those only the VC treatments *i* and *iv* were used (144 trees). Ammonium and nitrate ions were extracted with 2M KCl and analyzed by flow injection analysis and ion chromatography (FIA). Total C and N were determined by combustion (1100°C) and infrared detection on a LECO CNS-2000 analyzer (LECO Corporation, St. Joseph, MI, USA).

2.3.10 Data treatment

In the experimental design, treatments were randomized at each level (MSP, VC, fertilization), but the levels were not complete since fertilization was only done within certain MSP and VC treatments, and some soil variables were only measured in selected treatments. Responses were thus treated separately when appropriate. Mean growth from 12 trees per 0.25-ha subplot was compared across the eight sites by a mixed-effect analysis of variance, using MSP treatments and the control (5 levels), VC treatments (4 levels) and the interaction of MSP and VC as fixed effects, site ($n = 8$) and plot ($n = 40$) as random effects (indicative of the hierarchical design), with probability levels resolved by Restricted Maximum Likelihood (REML, see Searle *et al.*, 1992 ; Wolfinger *et al.*, 1994) and submitted to post-hoc Tukey HSD tests where justified. Absolute values of annual growth and the total cumulative 5-year (2004-2008) growth were thus analyzed for tree height and diameter. In addition, to further assess the effects of competition control on growth, the relative growth gain (RGG) was computed as the difference between the cumulative 5-yr growth of weeded (the most frequent VC, *iv*) and unweeded subplots (VC *i*) within a same MSP plot, divided by the growth of the unweeded subplot, and expressed as a percentage. It was inspired by the relative growth rate and other measures of relative growth presented by Hunt (1990). The RGG was submitted to an ANOVA and post-hoc Tukey HSD tests.

Shoot growth of fertilized trees (N and N+P fertilizations treated either separately or jointly) in years 5 and 6 was compared with that of unfertilized trees (the 12 tagged trees of section 2.3.6) through a mixed-effects analysis of variance; this was done separately for each selected MSP treatments and the control. Both annual shoot length and proportional height growth (current year's height divided by previous year's height) of fertilized trees were tested, again with mean growth per subplot.

Effects of MSP and VC treatments on soil properties (humidity, temperature, penetrability, chemical content, N mineralization) and foliar nutrition were analyzed through mixed models, similarly to tree growth, and separately for each variable. Sample sizes may have varied between variables (see particular sampling strategies above). Potential N mineralization of NH_4 and NO_3 was estimated as the difference between initial and final concentrations from *in situ* incubation tubes.

Survival of trees was recorded as alive (0) or dead (1) for all 1884 trees during the biannual growth surveys. Mortality was further assessed by noting time since death, in years (either 0 (still alive) or dead for 1, 2, 3 or 4 years). Both were individually compared with silvicultural treatments through a generalized linear mixed model (GLMM) fitted with the Laplace method of likelihood approximation (Bolker et al., 2009). Site and plot were added as random effects, as in the growth mixed model above, but here subplot (n = 157) was added as well in order to simulate correlation among trees within the same 0.25-ha subplot. Survival data was best represented with the binomial distribution while time since death was best represented with a Poisson distribution, for which overdispersion ($\hat{c}$, variance divided by the mean) was satisfyingly verified prior to GLMM analysis by fitting a simple linear model without random effects.

Statistical analyses were conducted with the R software (R Development Core Team, 2009), using a significance level of $\alpha = 0.05$. General linear mixed models were constructed with the "nlme" package and GLMMs with "lme4".

2.4 Results

Height growth of 5-year-old hybrid poplars was enhanced by mechanical soil preparation (MSP) prior to planting. There was a significant difference between the different MSP treatments and the control (Fig. 2.2, Table 2.2). The best growth was obtained in the following order: mounding > harrowing > heavy disk trenching > light disk trenching > unprepared (control). Unprepared plots produced trees significantly shorter than all other MSP treatments (Fig. 2.2). Growth in diameter at breast height (DBH) responded to MSP treatments very similarly to height growth (Fig. 2.3, Table 2.2). The gradient of the effect of MSP on height and diameter growth was likewise observed on annual growth (data not shown). In early years the difference was most evident when comparing the most intensive treatment with the least intensive, i.e., mounding and unprepared. The first treatment produced annual shoots of at least twice the length of the latter. Intermediate treatments were relatively similar in the first year, and only started differing later on. Any MSP treatment, even the least intensive (light disk trenching), significantly reduced mortality in hybrid poplars (< 5%) compared with the absence of preparation, where mortality rates were over 20% and trees died early after planting (Fig. 2.4). MSP also reduced the ground cover of competing shrubs and herbaceous plants significantly compared with plots that were not mechanically prepared prior to planting (e.g., herbaceous cover in unprepared plots = 25.4%, SE = 2; in other MSP treatments = 9-15%, SE = 2; $P < 0.05$).

Vegetation control (VC) by removal of aboveground parts of competing herbaceous and woody vegetation increased height and diameter growth of trees (Fig. 2.2 and 2.3, Table 2.2). The different frequencies of VC affected growth in the following order: at years 2, 3 and 4 > at year 3 > at years 2 and 4 > never (Fig. 2.2 and 2.3). There was no significant interaction between MSP and VC in the absolute values of tree height and diameter growth (MSP x VC, in Table 2.2). Nevertheless, the relative gain in height growth due to VC (RGG, which compared the two most extreme VC frequencies, *i* and *iv*) varied significantly depending on MSP, ranging from 25% with mounding to greater than 200% in unprepared plots (Fig. 2.5). Diameter RGG, on the other hand, did not vary between MSP treatments.

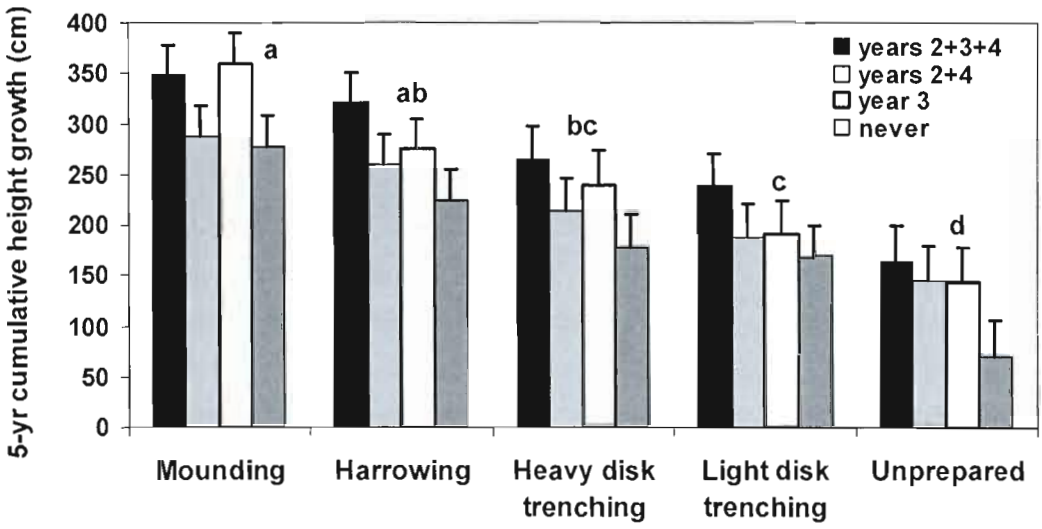

Figure 2.2 Effect of mechanical soil preparation (MSP) and vegetation control (VC) on height growth (cumulative 5-yr height growth) of hybrid poplars across four different MSP treatments and the control (unprepared). Values are means of trees from 8 sites, error bars are SE. MSP treatments and the control were all compared to each other through a post-hoc Tukey HSD, and different letters thus represent significantly different means at $\alpha = 0.05$. The two most extreme VC treatments (at years 1-2-3, and never) are significantly different within each treatment.

In the three selected MSP treatments where it was applied, there was no significant difference between N fertilization and N+P fertilization ($P > 0.3$; data not shown). Therefore, all subsequent references to "fertilized trees" combine both types of fertilization. Annual shoot growth of fertilized trees was higher than that of unfertilized trees during the year of fertilizer application (i.e., year 5). However, it was only significant in the mounding treatment ($P = 0.009$; Table 2.3). During that year, trees on mounds that received fertilizers produced around 31% more shoot length, or grew 32 cm higher, compared with unfertilized trees (Table 2.3).

Table 2.2 Detailed results of the mixed ANOVA comparing hybrid poplar height and diameter growth with treatments of mechanical soil preparation (MSP) and vegetation control (VC) in a 3-level hierarchical design of site/plot/subplot. Subplot had no variance assigned to it because growth of individual trees was averaged within 0.25-ha subplots. %variance is the proportion of total variance provided by a given source of variation.

Source of variation	df	SSE	MSE	%variance	F-value	P-value
Height growth						
Fixed effects						
Mechanical soil preparation (MSP)	4	62,8326	157,081	72.8	19.4	< 0.0001
Vegetation control (VC)	3	146,272	48,757	22.6	6.02	0.000696
MSP x VC	12	23,840	1,987	0.9	0.245	0.995
Random effects						
Block	7	15,582	2,226	1.0		
Plot	28	67,620	2,415	1.1		
Residuals	102	345,931	3,391	1.6		
Total	156					
Diameter growth						
Fixed effects						
Mechanical soil preparation (MSP)	4	4,126	1,032	59.7	13.1	< 0.0001
Vegetation control (VC)	3	1,798	599	34.6	7.58	< 0.0001
MSP x VC	12	242	20	1.2	0.256	0.995
Random effects						
Block	7	190	27.1	1.6		
Plot	28	1,243	44.4	2.6		
Residuals	102	746	7.31	0.4		
Total	156					

Proportional height growth (current year height divided by previous year height) of fertilized trees also improved significantly in mounded plots. Harrowed trees also responded, albeit only slightly, to fertilizers when considering the proportional gain in growth ($P = 0.054$). Trees in both mounding and harrowing plots again showed greater annual shoot growth due to fertilization the following year (i.e., year 6). However, mounding was again in year 6 the only treatment to clearly respond in proportional height growth ($P = 0.023$; Table 2.3). Trees in unprepared plots did not respond favorably the years following fertilization. Despite varying growth results, fertilization significantly enhanced leaf mass and leaf N content in the tested MSP treatments and the control (Table 2.3).

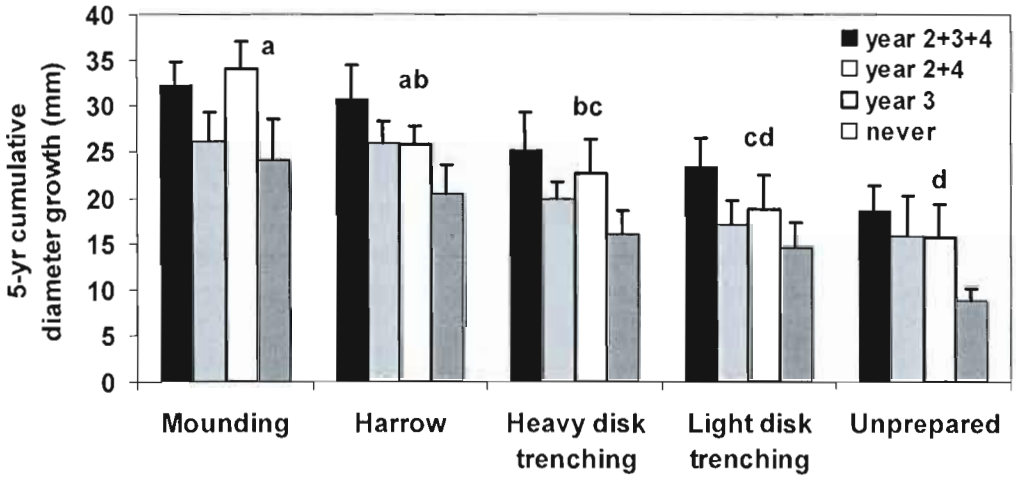

Figure 2.3 Effect of mechanical soil preparation (MSP) and vegetation control (VC) on cumulative 5-yr diameter growth of hybrid poplars across four different MSP treatments and the control (unprepared). See Fig. 2.2 for statistical details.

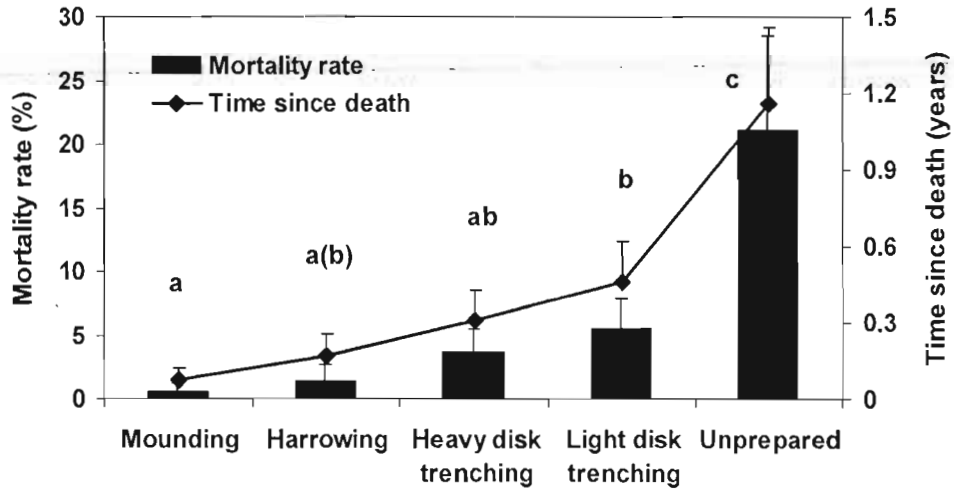

Figure 2.4 Mortality rate (%) and time since death (TSD; in years) per mechanical soil preparation (MSP) treatment and the control (unprepared). A higher value of TSD implies that a tree died early. Values are means of trees from 8 sites, error bars are SE. MSP treatments and the control were all compared to each other through a post-hoc Tukey HSD, and different letters thus represent significantly different means at $\alpha = 0.05$ (letters apply to both mortality rate and TSD, which vary equally along the MSP gradient); a letter in parentheses implies a marginal difference ($0.05 < P < 0.1$).

Table 2.3 Effect of fertilization (N and N+P combined) on annual (2008 and 2009) shoot growth and proportional growth (current year height divided by previous year height) of hybrid poplars in two mechanical soil preparation (MSP) treatments and the control (unprepared). Values are means from all eight sites, with SE in parentheses. Probability that the growth of fertilized trees is higher than that of unfertilized trees is the result of an analysis of variance.

MSP	Shoot growth (cm)		Prob [Fert >	Proportional growth		Prob [Fert >
	Fertilized	Unfertilized	Non-Fert]	Fertilized	Unfertilized	Non-Fert]
Year 5						
Mounding	136.8 (10.5)	104.1 (9.1)	0.0094	1.53 (0.02)	1.38 (0.02)	0.0005
Harrowing	106.1 (11.8)	92.4 (12.4)	0.47	1.43 (0.03)	1.32 (0.04)	0.054
Control	67.2 (15.9)	58.4 (16.4)	0.68	1.43 (0.04)	1.36 (0.03)	0.28
Year 6						
Mounding	105.7 (5.9)	77.0 (10.4)	0.036	1.28 (0.02)	1.22 (0.01)	0.023
Harrowing	84.9 (5.7)	61.2 (7.1)	0.031	1.26 (0.02)	1.22 (0.02)	0.14
Control	67.4 (15.2)	91.1 (13.0)	0.22	1.31 (0.04)	1.27 (0.03)	0.40
Year 5	Leaf mass (g leaf^{-1})			Leaf N (mg g^{-1})		
Mounding	0.62 (0.03)	0.40 (0.01)	< 0.0001	23.3 (1.3)	18.3 (1.0)	0.0081
Harrowing	0.54 (0.04)	0.42 (0.03)	0.033	22.3 (0.9)	17.4 (0.9)	0.0019
Control	0.46 (0.04)	0.34 (0.03)	0.027	22.0 (0.5)	17.6 (0.8)	0.0006

Effects of MSP showed a tendency to increase soil temperature and penetrability, whereas a decrease in soil water content and total C and N concentrations (although the C/N ratio remained constant) was observed with increasing intensity of soil preparation treatments (Table 2.4). MSP treatments were relatively similar regarding potential mineralization rates of N (sum of NH_4 and NO_3). Availability of other elements, as well as pH, cation exchange capacity (CEC) and base saturation (BS), did not differ significantly between MSP treatments (data not shown). Mechanical soil preparation also reduced slightly the thickness of the residual, post-treatment organic soil layer (for the four MSP treatments, mean = 7.9 to 8.8 cm; SE = between 0.6 and 1.7; n = 8) compared with the undisturbed FH horizon in unprepared plots (mean = 10.1 cm; SE = 1; difference marginally significant at $0.05 < P < 0.1$). Competition control, in contrast, had no significant effect on soil variables (data not shown).

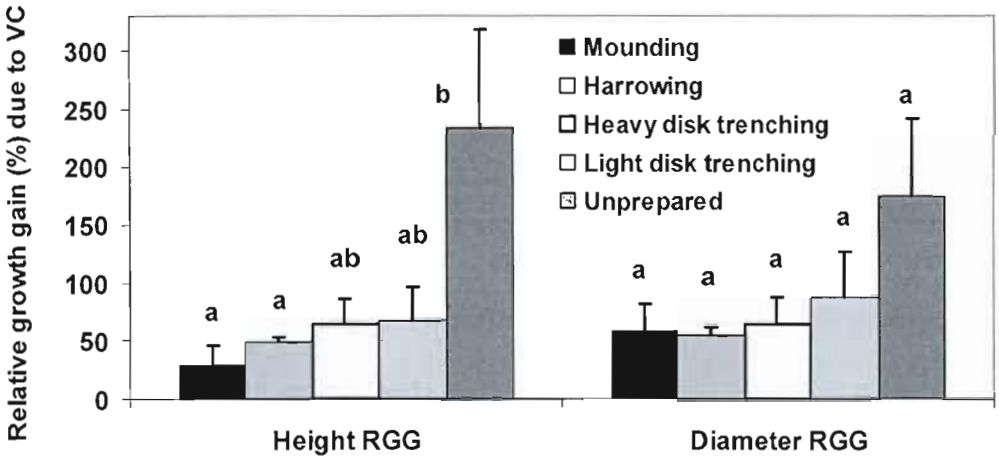

Figure 2.5 Effects of vegetation control (VC) on the relative growth gain (RGG, the difference between the cumulative 5-yr growth of weeded and unweeded subplots within a same MSP plot, divided by the growth of the unweeded subplot, and expressed as a percentage).

Table 2.4 Effects of mechanical soil preparation (MSP) on soil physical and chemical characteristics. Measures were taken in the first 20 cm of surface soil. Values are means across all eight sites, with SE in parentheses. For each soil characteristic, MSP treatments and the control were all compared to each other through a post-hoc Tukey HSD, and different letters thus represent significantly different means at $\alpha = 0.05$

	Mechanical soil preparation		
Soil variable	Mounding	Harrowing	Unprepared
Temperature, °C	14.8 (0.9) a	14.3 (0.6) ab	13.8 (0.5) b
Humidity, % vol. water	13.9 (1) a	21.5 (2) b	26.1 (2) b
Penetrability, cm	28.5 (2) a	21.1 (1) b	23.8 (2) ab
Total C, mg g^{-1}	15.4 (3) a	46.0 (6) b	80.1 (15) c
Total N, mg g^{-1}	0.797 (0.2) a	2.02 (0.3) b	3.44 (0.6) c
C/N	23.3 (3) a	23.3 (1) a	22.6 (0.9) a
Mineralized N, mg g^{-1}	0.0518 (0.02) a	0.0293 (0.01) a	0.0455 (0.02) a

Foliar nutrient content (mg g^{-1} of Ca, K, Mg, N, and P) during summer of all years varied across MSP treatments to different extents depending on the nutrient. Calcium and P foliar contents were similar among treatments, with ranges of 55-75 mg g^{-1} and 13-16 mg g^{-1} (and

P-values between treatments of 0.12 and 0.40, respectively). Foliar contents of K (84-123 mg g^{-1}), Mg (14-21 mg g^{-1}) and N (13-15 mg g^{-1}) varied significantly between MSP treatments, and usually with higher values in more intensive treatments producing better growth. Unprepared plots always showed the lowest values.

2.5 Discussion

The silvicultural treatments tested in this study, particularly MSP, affected several parameters that may in turn impact tree growth, such as above- and belowground competition, soil chemical, physical and biological properties, as well as the distribution of these properties in the soil. Moreover, the treatments interacted in important ways to modify those parameters.

This discussion will focus on each silvicultural tool separately, and will also include interactions when appropriate.

Considering the relatively harsh climatic and soil conditions in the region of study, these hybrid poplar plantations performed reasonably well when treated with the best available management tools (i.e., mounding). The highest growth obtained was slightly better than that of other studies on hybrid poplars conducted in forested sites of Quebec (Coll *et al.*, 2007 ; Guillemette et DesRochers, 2008 ; Sigouin, 2008), but not as good as in forested sites of Vancouver Island in western Canada (Brown et van den Driessche, 2005 ; van den Driessche, 1999), and fairly comparable to plantations established on agricultural sites in the transitional zone between the prairies and the boreal forest of central Canada (Pinno et Bélanger, 2009 ; Pinno *et al.*, 2009).

2.5.1 Mechanical soil preparation

The gradient of increasing height growth across MSP treatments paralleled the gradient of increasing MSP intensity. The slowest growth was obtained at unprepared plots that retained the original, undisturbed soil layers with a relatively thick organic layer. The best growth was found among the strongly disturbed mounds mostly made up of mineral soil with a buried

organic horizon, whereas intermediate growth was produced by varying intensities of organic and mineral soil mixing (i.e., harrowing and disk trenching). These results generally agree with previous studies on other tree species that reported greater benefit to growth from intensive MSP treatments (Landhäusser, 2009 ; Nilsson et Allen, 2003).

Another crucial benefit derived from MSP relates to the establishment and early survival of trees. In plots that were not mechanically prepared prior to planting, mortality of hybrid poplars was as high as 20%, a number also reported by Burgess et al. (1995). Moreover, many of these trees died early, in the first or second year after planting (as suggested by the higher time since death, Fig. 5; and S. Bilodeau-Gauthier, personal observation). In other MSP treatments, mortality was lower than 5% in general, and even absent in mounded plots. In an intensive management perspective, where the production of every single seedling involves substantial resources, MSP is therefore a necessity in Precambrian Shield settings characterized by coarse acidic soils.

The MSP treatments used in this study also had an impact on soil conditions. The more intensive MSP treatments reduced the soil water content, but this was apparently not sufficient to hamper tree growth. MSP created microsites favorable to tree growth and development, as emphasized by the present growth results and as predicted in other studies (Örlander, 1987 ; Sutton, 1993 ; Thiffault *et al.*, 2003). These favourable microsites were notably the consequence of improved soil penetrability and temperature. Soil temperature was similar in mounds and harrowed plots but higher than in unprepared plots, as also reported by Sigouin (2008). A higher soil temperature can have positive effects on soil N mineralization (Grenon et al., 2004). Grenon et al. (2005) even suggested that N mineralization rates were more important for tree growth than total soil N reservoirs. Here, mounds produced the same amount of mineralized N compared to other MSP treatments where more organic matter was preserved. In contrast, mounds were mostly composed of mineral soil, and exhibited the lowest total N content of all MSP treatments. Therefore, mounding might have seemed detrimental to tree growth because of this nutrient-poor and drought-prone mineral soil in which the tree is initially planted. Indeed, the removal of

nutrient-rich organic matter was shown to cause nutrient deficiencies and limit tree growth (Merino et Edeso, 1999), and Fang et al. (2008) recently highlighted the benefits of nutrient-rich organic material for hybrid poplar growth. Still, mounding created beneficial conditions for soil fertility since N mineralization was equal to that in other MSP treatments. Although this does not yet explain the greater growth yield attributable to mounding, at least it suggests that this MSP technique is possibly on par with others in regards to the N supply.

Because mounding created less compacted and warmer soil conditions than harrowing and the control, root development in early years could have been favored in mounds. This was shown through visual observation of root excavations undertaken within all MSP treatments and the control at the end of the first growing season (data not shown) and as revealed by a series of non-destructive root excavations undertaken during the fourth growing season on 45 trees within the mounding and control plots at all eight sites (Bilodeau-Gauthier et al., submitted). In these excavations, trees growing on mounds systematically had substantially larger root systems than trees from other MSP treatments. The well-developed root system on mounds could also explain the strong height response of the trees to an added nutrient supply. Early root development in mounds has indeed been shown to be a great asset for the subsequent success in height growth (Block *et al.*, 2006 ; Block *et al.*, 2009). In addition, the surface of mounds, with mineral soil exposed, was generally almost devoid of competing vegetation for a few years after the treatment (Bilodeau-Gauthier et al., personal observations). The upheaval and exposure of the mineral soil seemed to efficiently reduce colonization by competing species, a reduction that is a typical benefit of mounding treatments (Örlander et al., 1990).

Along the same lines, Messier et al. (2009a) observed, in a split-root pot experiment where half of the pot was covered with competing grasses while the other was bare, that fine-root biomass of hybrid poplars was highly sensitive to the presence of competing roots despite adequate supplies of water and nutrients. Also, Platt et al. (2004) observed positive responses in mountain beech (*Nothofagus solandri*) seedlings after root competition removal, with or without fertilizer additions, but no response to fertilization alone. This again suggests that

belowground competition for nutrients can be strong and that trees benefit from fertilization the most when competition is low (Kabba et al., 2007).

Furthermore, the underlying – and undisturbed – organic horizon over which the mound was formed might represent a reservoir of nutrients available to the tree once the roots are deep enough. Because former vegetation is buried and possibly destroyed when mineral soil is upturned to form the mound, this potential reservoir is probably relatively devoid of competing roots from other plants. Although the data presented in this paper showed the mound surface soil to be less fertile than in other MSP treatments, further investigation of deeper horizons will possibly reveal yet another benefit of mounding.

2.5.2 Competition control

Competition control increased the height and diameter growth of hybrid poplars, which is in accordance with previous reports on aboveground vegetation removal for hybrid poplars (Czapowskyj et Safford, 1993 ; mowing treatments of Pinno et Bélanger, 2009). It should be noted, however, that the competition control treatments used here did not totally eliminate the competing vegetation as opposed to other studies using herbicides or soil cultivation (Coll *et al.*, 2007 ; Pinno et Bélanger, 2009 ; Sigouin, 2008). Notably, Coll et al. (2007) reported that 2-yr-old hybrid poplars planted at formerly forested sites gained nothing from mechanical removal of aboveground plant parts, while there were great benefits from herbicide applications that targeted competing roots. They thus concluded that competition was strongest for soil nutrients at these sites and that competition control treatments needed to aim at belowground plant parts. Nonetheless, shoot removal certainly also impacts belowground plant parts by killing fine roots (Comas et al., 2000) and by limiting water uptake.

The present study revealed responses of tree growth to aboveground competition control that differed when combined to other silvicultural management tools. Admittedly, this was not apparent when looking at absolute values because the interaction term in the mixed analysis of variance was not significant. However, by comparing relative growth values of trees in weeded and unweeded plots, it appeared that the relative growth gain (RGG) due to VC

varied according to MSP treatment, but only for height and not diameter. Indeed, the effect of competition control on hybrid poplar growth was stronger in the less intensive MSP treatments. In unprepared plots, mean height growth of weeded hybrid poplars was more than 2-fold (200%) that of the unweeded trees, while in mounding plots the RGG due to VC was only around 25% (Fig. 4).

A similar conclusion was reached by Burgess et al. (1995) after 7 years in *Pinus strobus* and *Picea glauca* plantations in Ontario, Canada. This emphasizes the idea that MSP itself is an efficient approach to limiting competition for resources (Pehl et Bailey, 1983 ; Ross et Walstad, 1986). As a result, removing plant competition where it has previously been reduced by MSP has much less impact on the development of target trees. Analogous to that are the results of Pinno and Bélanger (2009), who reported that competition control was less effective on unproductive, nutrient-poor sandy sites where competition for soil resources was naturally low. In a study on pine plantations, Nilsson and Allen (2003) observed that loblolly pine growth was enhanced in early years due to herbicide control of competing vegetation.

Because VC had no significant effect on soils, and because removal of aboveground parts of plant competitors mainly impacts aboveground competition, the effects of VC on tree growth reported in the present study should represent mostly the response of trees to changes in light competition intensity. When competing vegetation is controlled only at year 3, it has similar or slightly greater benefits for hybrid poplars than control at years 2 and 4. This suggests that a silvicultural intervention at that time is not optimal, and that the better results of the third-year brushing treatment would represent a more efficient improvement in light availability from competition removal.

2.5.3 Fertilization

Fertilization can provide a substantial improvement in short-term growth, as suggested by the ~30% improvement in height growth observed in fertilized trees during the application year (Table 3). This is similar to other reports of hybrid poplar production gains from fertilization of 21% (Brown et van den Driessche, 2002 ; Heilman et Xie, 1993), 40% (Coleman et al.,

2006), or even 62% (Czapowskyj et Safford, 1993). Yet, in some very nutrient-limited plantations, gains as high as 200% in tree biomass were obtained (Coyle et Coleman, 2005). Nonetheless, it does not seem to be universally effective since in this study the improvement was significant only on mounds. Some explanations for this include 1) the advantage of a larger root system in mounds (see discussion below) that could allow quick and efficient absorption of the nutrient input, and 2) the uptake of N and P by competing herbaceous plants in the other MSP treatments or unprepared plots (see herbaceous cover data in the results section). Overall, the results suggest that fertilization may not be sufficient to compensate for inadequate soil preparation. This was also proposed by Nilsson and Allen (2003), who observed no effect of fertilization (at planting) in low intensity MSP treatments, while in intensive MSP treatments it positively influenced tree growth in later years, after crown closure. Shiver et al. (1990) compared silvicultural treatments on Spodosols (Podzols) with more fertile soil types, and concluded that fertilization and competition control had more lasting effects on the acidic, nutrient-poor Spodosols.

In the present study, combining N with P fertilizer additions did not result in greater growth, despite the fact that P was found to be important in certain ecosystems (Abel *et al.*, 2002 ; Trichet *et al.*, 2009). There has also been reports on the benefits of combining N and P in other, possibly more nutrient-deficient stands (Blevins et al., 2006), notably some aspen (*Populus tremuloides*) plantations in western Canada (van den Driessche et al., 2005) and cottonwood clones in Washington State, USA (DeBell et al., 1990). In a study that combined competition control and fertilization, Borders et al. (2004) observed increased growth due to competition control in the early years, while fertilization had lasting effects on growth enhancement. In their fertilization trial, Amateis et al. (2000) measured only the height of dominant trees and, as a result, they could not observe fertilizer effects on less than optimally developed trees, as we managed to do here with trees in unprepared plots. Higher leaf mass and N content after fertilization are in accordance with previous studies (Coleman *et al.*, 2006 ; Zhang et Allen, 1996 ; Zhang *et al.*, 1997).

2.6 Conclusion

The results of this study have important implications for future management strategies of hybrid poplar plantations in boreal regions. The different techniques and management tools used here interacted, with varying effects depending on the site conditions induced by the treatments, in ways that can influence the decision of using those techniques or not. Still, other considerations (e.g., socio-economical) might further influence the decision process.

Based on our results, we propose that forest managers prioritize their management interventions as follows: mechanical soil preparation > aboveground vegetation control > fertilization. We suggest this sequence because MSP has the greatest impact in creating favourable soil microsites for planting, in reducing competing vegetation previously on site, and in promoting tree establishment, survival and growth. VC and fertilization, as applied in this study, could not compensate for inadequate MSP. When both of these treatments were undertaken at unprepared sites, trees were about half the height of those on mounds with neither VC nor fertilization.

The present results and suggestions are in line with the few other studies that encompassed similar ranges of interacting tools, albeit with different tree species in different environments (Carter et Foster, 2006 ; Nilsson et Allen, 2003 ; Zhao *et al.*, 2009). Among the MSP treatments, mounding appears to offer better early results due to rapid root development, high seedling survival, and substantial N mineralization. In addition, its effects were still observable after several years. The high sensitivity of hybrid poplar roots to belowground competition may explain why MSP is so critical to this species. In conditions where some VC is considered necessary, it could be done only during the second year after planting to minimize the cost and maximize the results. Finally, fertilization should be considered only if intensive MSP is also done.

2.7 Acknowledgements

This study was funded by the Fonds québécois de recherche sur la nature et les technologies through a research grant to C. Messier et al. (project #2007-FO-118127), as well as a Ph.D. scholarship to S. Bilodeau-Gauthier. Further funding was provided to D. Paré by the Programme de mise en valeur des ressources du milieu forestier, volet 1, of the Ministère des Resources naturelles et de la Faune du Québec (MRNFQ) and the Quebec Intensive Silviculture Network (RLQ). Early contributors to this project's establishment also included D. Cormier (FERIC), W. H. Hendershot (McGill University), P. Périnet (MRNFQ), and G. Prégent (MRNFQ). The authors wish to acknowledge the essential participation of Louisiana-Pacific Corp., Chambord, QC division, and their dedicated poplar coordinator C. Lavoie, in lending lands and workforce for tree planting, machinery for soil preparation, and overall for their openness to experimentation. Another instrumental partner was the MRNFQ, particularly P. Périnet and A. Fauchon for advice regarding poplar clones, and J.-P. Girard for making possible the fertilization experiments. Further credits go to P. Gagné and B. Bigué from the RLQ for their contribution and coordination of the project. Protocol and field sampling of competition cover were the result of efforts by S. Fortier. Field work was made possible thanks to the help of P. Gagné, L. St-Antoine (CFS), A. Beaumont, S. Reynolds, and A. Turgeon.

CHAPITRE II

HOT SPOTS FOR ROOT GROWTH CREATED BY MECHANICAL SOIL PREPARATION OPTIMIZE HYBRID POPLAR NUTRITION IN POOR BOREAL SOILS

3.1 Abstract

Background and Aims
The successful establishment of fast-growing trees could be particularly dependent on competition from roots of other plant species for belowground resources. Soil disturbance from mechanical soil preparation creates favourable microsites for root growth but potentially diminishes soil nutrients.
Methods
Root growth and distribution were compared with soil nutrient availability across soil profiles of mechanically prepared (mounding) and unprepared soil microsites for young hybrid poplar trees.
Results
Hybrid poplars on mounds developed larger and more abundant roots than in unprepared soils. Hybrid poplar roots avoided the nutrient-rich forest floor layer at the surface of unprepared soils where numerous live roots from other species were found, while they proliferated in the buried forest floor layer and in the exposed surface mineral layer of mounds with a lower nutrient availability but devoid of other live roots. Root growth benefited from the warm, less compacted soil of mounds, providing access to a larger soil volume and greater soil nutrient amounts.
Conclusions
Better tree growth on mounds was due to soil conditions favouring a greater root development for planted hybrid poplars, including a reduction in resource and non-resource belowground competition with other species. In addition, creating such conditions in tree plantations may be an alternative to more labour-intensive, time-consuming, or environmentally-damaging vegetation control methods.

Keywords: hybrid poplar, mechanical soil preparation, nitrogen, root competition, root growth. 3.2 Introduction

3.2 Introduction

Hybrid poplar in short-rotation plantations can achieve high yields because of genetic enhancement programs and intensive silviculture management techniques (Ceulemans et Deraedt, 1999 ; Ceulemans *et al.*, 1992 ; Strobl, 1987). However, *Populus* species and clones are sensitive to competition. As shade-intolerant species, they are known for their sensitivity to aboveground competition for light (Messier *et al.*, 1998). Yet, as pioneer species, hybrid poplars also seem to be intolerant of belowground competition for nutrients, and space (Messier *et al.*, 2009a).

For numerous plant species, belowground competition is often more important than aboveground competition (Casper et Jackson, 1997). It can be an important obstacle to the establishment of tree plantations (Balandier *et al.*, 2007 ; Collet *et al.*, 2006 ; Nambiar et Sands, 1993) or natural forest regeneration (Devine et Harrington, 2008 ; Doležal *et al.*, 2006 ; Kueffer *et al.*, 2007), thus requiring adequate management techniques (Balandier *et al.*, 2006). For instance, roots of neighbouring grasses were shown to reduce root development, stem growth and survival of *Populus tremuloides* by lowering soil temperature, competing for resources (including space), or emitting allelopathic compounds (Landhäusser et Lieffers, 1998 ; Landhäusser *et al.*, 2007).

Therefore, early root development of the target species is a fundamental factor in the successful establishment of plantations, favouring juvenile tree growth and survival (Burdett *et al.*, 1983 ; Grossnickle, 2005 ; McCreary et Duryea, 1987). Hibbs et al. (2003) attributed the high yields of hybrid poplars planted on the poorly drained, non-irrigated soils of the Willamette Valley of western Oregon to their deeply and extensively developed root systems.

Mechanical site preparation (MSP) usually has a beneficial impact on tree growth (Thiffault *et al.*, 2003) despite the fact that it exposes mineral soils that are generally poorer in nutrients than the surface organic layers (Gastaldello *et al.*, 2007). Örlander et al. (1996) observed long-term benefits of MSP on the growth of Scots pines (*Pinus sylvestris*), even though the mechanically prepared soils had much lower C and N content. This is in agreement with

recent observations on hybrid poplars (Bilodeau-Gauthier *et al.*, 2011) where better growth of this fast-growing tree with high nutrient requirements was also found on disturbed soils that showed much lower C and N content at the surface, despite a N growth limitation demonstrated by fertilization. There are likely many mechanisms by which mechanically-induced soil disturbance improves tree growth and their respective importance is still poorly understood.

Soil disturbance can modify the spatial distribution of soil nutrients, for instance by amalgamating nutrients in patches. Root growth may show plastic response to nutrient-enriched soil patches (George *et al.*, 1997 ; Hodge, 2006), which may optimize root foraging and efficient scavenging of resources in heterogeneous soils (Hodge, 2004). Numerous studies have focused on root plasticity of agricultural crops and herbaceous species in response, for instance, to spatial distribution of N. However, there have been fewer studies on tree species (Hawkins et Metcalfe, 2008, with Douglas-fir). One study by Heineman et al. (1999b) focused on spruce growing on mounds in western Canada. They analyzed vertically the soil and roots, but they delimited vertical sampling layers based solely on depth, rather than by soil horizon types as advocated by Strong and La Roi (1988). In this respect, their results cannot be used to distinguish root foraging strategies for the optimal preference of soil material in which to proliferate.

The present study proposes a unique assessment of the spatial distribution of hybrid poplar roots in relation to the type of soil material (either mineral or organic) explored. Root excavations were undertaken within experimental plantations of hybrid poplars in the boreal forest of Quebec, Canada, and at sites that received two contrasting treatments resulting in different vertical arrangements of soil layers, i.e., mechanical soil preparation by mounding and an unprepared control. The objectives were 1) to evaluate the development of the root system by measuring the abundance, diameter, and location of proximal roots, as well as 2) to analyze N dynamics in the different soil layers. It was hypothesized that *i*) hybrid poplar roots would avoid areas containing live roots from other species, and that *ii*) soil N mineralization and availability would be enhanced by the soil disturbance resulting from the mounding process. The results should help in understanding the response of hybrid poplar trees to the

spatial distribution of soil resources and to the presence of root competition, as well as in improving the efficiency of silvicultural treatments such as soil management.

3.3 Methods

3.3.1 Sites and experimental design

Eight formerly forested sites were chosen in the Saguenay–Lac-St-Jean region (between 71° 05' and 72° 52' W, and between 48° 08' and 48° 43' N) of the province of Quebec, Canada. These sites are situated in the southern boreal forest. Original stands consisted of balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), black spruce (*Picea mariana*), white spruce (*Picea glauca*) and paper birch (*Betula papyrifera*). Soils are representative of Precambrian Shield settings characterized by coarse acidic soils, and are classified as Orthic Ferro-Humic Podzols (Canada Soil Survey Committee, 1992) or Haplorthods (Soil Survey Staff, 1998). A description (thickness and depth) of the different soil layers is provided in Table 3.1, where the unprepared treatment is representative of natural conditions. Mean annual temperature for this region is 2.2°C and mean annual precipitation is 1000 mm (of which 710 mm is rainfall), while mean summer (June-September) temperature is 15.5°C and mean monthly summer precipitation (rainfall) is 107.5 mm (Environment Canada, 2009).

This study was undertaken among experimental plantations that are described elsewhere in greater detail (Bilodeau-Gauthier *et al.*, 2011). Following whole-tree harvesting in the summer of 2002, soils were mechanically prepared in the fall of 2003. Bare-root, ~ 1-m-tall hybrid poplar tree cuttings of the 915319 clone *Populus maximowiczii* x *Populus balsamifera* (Périnet *et al.*, 2001) were obtained from a nursery operated by the Ministère des Ressources naturelles et de la Faune du Québec at Grande-Piles, QC, Canada. The cuttings were produced in the spring from parent trees in the nursery plantations, and cultivated over the summer in irrigated, fertilized, and weeded soil. This allowed them to develop a substantial root system, which was subsequently groomed in the fall when the cuttings were dormant, a state in which they were kept until shipping to the field the next spring. The bare-root cuttings were hand-planted with a shovel in April 2004 at a depth of 20-30 cm and in straight

rows at a spacing of 3 x 3 m (density = 1100 trees ha^{-1}). Throughout this text, the year of planting will be considered as year 1.

Two soil treatments were compared: 1) MSP by mounding and 2) a control where the soil was left unprepared. Mounding is a common MSP treatment in Scandinavia and Canada (Örlander *et al.*, 1990 ; Sutton, 1993). For this study, it was done using a backhoe equipped with a 45-cm-wide bucket that dug into the soil through the forest floor and down to a depth of 60 cm to retrieve the mineral soil (i.e, the B horizon). The mineral soil was then upturned over undisturbed soil to form a mound of about 30 cm in height and 50 cm in radius. The mound buried the original forest floor material and covered the vegetation beneath it. Tree cuttings were planted directly on the mound, slightly on the side, ideally down to a depth of 20-30 cm so that the rooted end of the tree cutting reached the buried forest floor layer. Trees in the unprepared plots were planted at the same depth as those on mounds (when possible, since unprepared soil was not as easily penetrated as the soil of mounds, see penetrability measures in Bilodeau-Gauthier *et al.*, 2011). Figure 3.1 provides a schematic description of mounding and Table 3.1 illustrates the vertical soil profile of the two treatments. It must be noted that the upper mineral layer in the tree's immediate environment is not as thick as the highest point of the mound since the tree is planted on its side. Each treatment covered a 1 ha plot and was repeated at each of the eight sites, hence $n = 8$. The 1 ha plots were further divided into four equal subplots (0.25 ha) where different vegetation control (VC) schedules were tested (including no vegetation control, hereafter called the unweeded subplots). Only the most frequent VC treatment (vegetation controlled once a year during the first 3 years, hereafter called the weeded subplots) was used for root excavations and soil analysis, while root ingrowth bags (see below) were installed in both the weeded and the unweeded subplots.

In the boreal forest, plant roots mainly colonize the first 15 cm of soil (Strong et La Roi, 1983), i.e., within the surface organic soil, also called forest floor (Paré et Bernier, 1989), or at the interface of the organic and mineral layers (Strong et La Roi, 1985). Bauhus and Messier (1999b) showed that the forest floor of the southern boreal forest was densely populated by plant roots. They also acknowledged that root competition in this ecosystem must be high. In addition, observations made during the root excavations undertaken in the

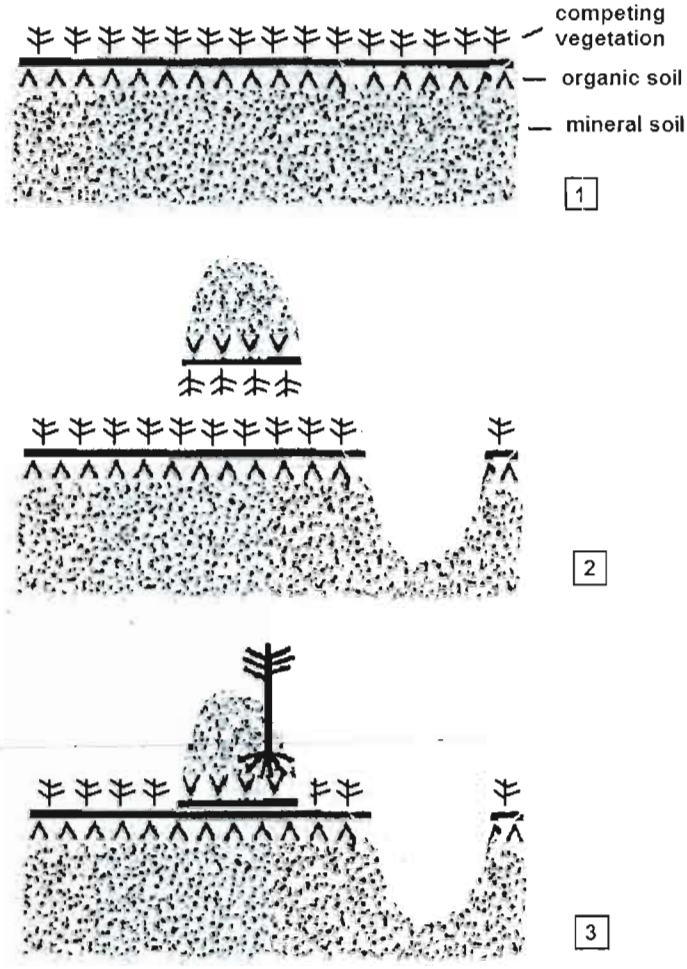

Figure 3.1 Schematic representation of the making of a mound (inspired by Sutton, 1993). 1) A portion of the undisturbed soil – covered with competing herbaceous and woody vegetation – is dug out; 2) the dug out soil matter is inverted; and 3) placed nearby over the undisturbed forest floor, thus covering and killing the competing vegetation. The tree is planted slightly on the hillside of this mound.

course of the present study have confirmed that in unprepared soils, the majority of plant roots were located within the forest floor (Bilodeau-Gauthier et al., personal observation). Therefore, the unprepared forest floor was considered a highly competed for environment. On the other hand, the buried forest floor within the mound was considered as being mostly devoid of live roots from competing plants, because the latter were completely covered by the mineral soil displaced to create the mound and consequently the competing plant roots were presumed dead. This assumption was based on the typical competition-reducing effect of mounding (Nilsson et Örlander, 1999) and other mechanical soil disturbance (Peltzer *et al.*, 2000).

3.3.2 Root excavations

In July of year 4, 45 3-year-old hybrid poplar trees were randomly chosen in the mounding treatment (24 trees, three per site across the eight sites) and the unprepared control (21 trees, three per site at seven sites). These trees were not the same trees that were used for soil sampling or for root ingrowth cores, for which undisturbed soil was needed. Roots were partly excavated in a non-destructive manner. Digging was done by hand in a 30-cm radius around the base of the trees and down to the stump end (see maximum rooting depth in Table 3.1). Such partial excavations allowed us to maintain the tree stability and spatial arrangements of roots. The excavation process exposed all roots that started from the stump (hereafter called proximal roots, which are assumed to subsequently branch into several smaller roots).

Diameter at the base (where it protruded from the stump) of every proximal root was measured with an electronic calliper. It should be noted that a proximal root can be of any diameter, and thus proximal diameter here ranged from close to 0 mm to over 30 mm. The measure of proximal root diameter was used because a previous study had demonstrated, through complete excavation of root systems and numerous measurements of root architecture and physiology, that proximal root diameter of hybrid poplars was strongly and linearly related to other root characteristics (Domenicano *et al.*, 2011). The authors successfully built linear equations (R^2 = 0.6 to 0.8, $P < 0.0001$) linking proximal root

diameter to root length, root biomass and number of links, thus suggesting that non-destructive, partial excavations were adequate to acquire such information. The root systems excavated by these authors came from 2-year-old hybrid poplars of clone types (913313 and 913311, both *P. maximowiczii* x *balsamifera*) that were closely related to that of the present study. Consequently, the proximal root diameter determinations can be considered as an appropriate proxy for total root biomass and architecture (Oppelt *et al.*, 2001 ; Spek et van Noordwijk, 1994 ; Van Noordwijk et Purnomosidhi, 1995).

In addition to measuring the diameter, the depth (from the soil surface) at which a proximal was located was noted with a measuring tape. The fact that the hybrid poplar cuttings were planted deeply into the soil, as well as their capacity to produce roots from the whole length of the cutting that is belowground and not just the already-rooted bottom end, meant that proximal roots extended relatively horizontally from the stump and simplified the identification of the soil layer they explored. Thickness and location of the forest floor and mineral soil horizons were also noted for every tree to later build an average vertical soil profile for each treatment (Table 3.1). After measurement, the soil was gently filled back in to cover the roots. Total stem height and annual shoot lengths of the 45 excavated trees were measured with a measuring pole and tape. Stem diameter was measured with an electronic calliper, at mid-breast height (65 cm from the ground) because some trees were too short to allow measuring at the usual 1.3 m.

For every tree, the sampled proximal roots were classified by diameter (0-2, 2-10, 11-20, and 21-30 mm) and by the soil horizon in which they were found. Thereafter in this text, roots will be mainly referred to according to their diameter class, rather than to other common terms such as "fine roots" or "coarse roots". First, such terms imply that the function of said roots is known – which is usually not the case when only considering root diameter. Second, there seems to be no final consensus on what exact diameter should fine roots be; the most common range is 0-2 mm, but 0-1 mm has also been proposed, while some authors even argue that the roots whose function strictly covers nutrient uptake are those under 0.5 mm in diameter.

Table 3.1 Typical vertical soil profiles of the two mechanical soil preparation treatments (mounding and unprepared) describing the soil horizon types and their thickness. Soil horizons are presented, from top to bottom in the table, as they are found in the field in the tree's immediate environment. Maximum depth reached by roots corresponds to the deepest location of a root as observed in the field root excavations.

Soil horizon or material	Thickness (cm)	SE
Mounding		
Upper mineral	16.0	2
Buried forest floor	7.5	2
Lower mineral	7.8	2
Max depth reached by roots	31.3	2
Unprepared		
Surface forest floor	10.8	1
Lower mineral	10.5	1
Max depth reached by roots	21.3	1

Calculations were made for average diameter of proximal roots per tree, number of proximal roots per tree and per diameter class, and number of proximal roots per soil horizon (forest floor *vs* mineral soil). Also, the number of roots per cm of soil depth was obtained by dividing the absolute number of roots per tree by the average thickness of soil horizons. The ratio of tree height over the product of average root diameter and total number of roots (thereafter referred to as height: root ratio) was also computed. All root variables were compared between the two treatments using mixed analyses of variance with site as a random variable.

3.3.3 Root ingrowth cores

In October of year 4, 30-cm-long plastic mesh bags were installed 30 cm from the base of six trees per subplot in the mounding MSP treatment and the control, as well as under two distinct competition levels (i.e., in the weeded and unweeded subplots, see above at *Sites and Experimental Design*). Bags were filled with sifted mineral soil taken on-site but outside the plots. Ingrowth cores can provide reliable results, given that the soil the mesh bags are filled

with is similar enough in N content compared with the surrounding soil (Steingrobe *et al.*, 2000). Roots were then allowed to grow for 10 months and were collected in mid-August of year 5. Ingrowth cores were opened in the laboratory and roots were separated from soil by the immersion-and-flotation method, and then dried at 70°C for 48 h and weighed. Roots were not separated by species, and therefore roots could be from both hybrid poplars and competing species. Ingrowth core data should therefore be viewed as representing potential root growth, of all species present, under particular MSP treatments and competition levels.

3.3.4 Soil analyses

Potential N mineralization was assessed by comparing nitrate (NO_3) and ammonium (NH_4) concentrations at the start and at the end of 6-week (from the beginning of July to mid-August) *in situ* incubations undertaken at three different soil depths, i.e., 0-15 cm, ~20 cm, and for mounds also ~30 cm, at a distance of 30 cm from the base of three trees in the weeded 0.25 ha subplot of the mounding treatment and the unprepared control at the eight sites (45 trees, 114 incubations, n = 8 for mounding and 7 for the control). The 0-15 cm incubations were conducted in year 4 with 20-cm-long and 5.8-cm-wide closed-top PVC tubes as described in Brais et al. (2002b), Delphin (2000), and Raison et al. (1987), where both the initial and final soil samples were obtained by inserting the tubes into the surface soil. The ~20 and ~30 cm incubations were done in year 5 using incubation bags. In this case, initial soil samples were obtained by extracting with a soil auger approximately 1 kg of soil material at the two depths and at a distance of 30 cm from the base of the same trees as was done for the surface incubation above. Final soil samples were obtained by burying polyethylene bags filled with a similar quantity of soil at the same depths. Bags were tightly closed to prevent leaching induced by percolating waters (Brais *et al.*, 2002b ; Delphin, 2000). For both the bag and tube soil samples, NH_4 and NO_3 were extracted with 2M KCl (Maynard *et al.*, 2007) and analyzed by flow injection analysis and ion chromatography (FIA; Lachat Instruments, Milwaukee, WI). During the initial tube sampling, a small fraction of each sample was dried and ground to provide total C and N concentrations, which were determined on a LECO CNS-2000 analyzer (LECO Corporation). Soil incubations provide an estimate of the soil potential for N mineralization. Being mostly closed to outside influences

that could alter nutrient concentrations (e.g., water flow, root uptake), yet subjected to *in situ* temperature conditions, incubations constitute a snapshot of the activity of the microorganisms that degrade soil organic matter, which releases N into inorganic forms more readily accessible to plants (mostly NH_4, in the type of soils studied here). Soil microorganisms use this inorganic N themselves, therefore the concentrations found at the end of the incubation period are considered as the N mineralized in excess of microbial demand.

Soil concentrations of NO_3 and NH_4 were assessed in year 5 with ion-exchange resins (Plant Root Simulators, or PRS^{TM}-probes, Western Ag Innovations, Saskatoon, SK, Canada). The ion-exchange resin of these probes is a thin membrane (1.5 cm × 5.5 cm in surface area) contained in a small plastic probe (3 cm x 15 cm) that can be inserted into the soil with little disturbance. Resins were vertically installed at three soil depths, i.e., 0-5 cm, ~20 cm, and ~30 cm, during the same 6 weeks and at the base of the same trees as the incubations (48 trees, 144 resins, $n = 8$). During the burial period, the resins continuously adsorb soil nutrient ions that are flowing to the probe through the soil solution. The amounts of nutrients trapped by the resin represent the nutrient supply rate from freely flowing water to a specific soil location within the soil profile during a specific burial time period. It is a dynamic measure of ion fluxes in the soil over time, rather than a static measurement at a particular point in time like more conventional extraction methods (Qian et Schoenau, 2002). Several previous studies in agronomy and forestry have successfully used PRS^{TM}-probes to assess soil nutrient availability (Adderley *et al.*, 2006 ; Coll *et al.*, 2007 ; Fortier *et al.*, 2010b).

Soil temperature was measured at the base of each tree with a hand-held 20-cm electronic thermometer probe. Measurements were taken across all sites between June and August of year 4, and were repeated 2-3 times over the season for each tree, approximately once per month. This repetition allowed verifying that temperature measurements were consistent among individual trees. Data-logging temperature sensors (Maxim Integrated Products, Sunnyvale, CA, USA) were also placed at two sites (30 data-loggers per site), where soil temperature was measured every 2 hours from the beginning of June to the end of October of

year 4 at depths of 2, 10 and 20 cm. The sensor data were compared with the hand-held thermometer probe measurements to further verify the reliability of the latter unit.

3.3.5 Statistical analyses

Soil data by depth were compared between mounding and the unprepared control, while the difference in soil data between the three depths was evaluated within individual treatments. Both used mixed analyses of variance with site as a random variable. Nitrogen mineralization was calculated as the difference between the final and initial incubation inorganic N measurements. The amount of mineralized N was further estimated for the total soil volume. This volume differed between the two treatments. It was schematically represented as a cylinder with a 50-cm radius surface area (the size of a mound) and a length corresponding to the location of the deepest proximal root (see Table 3.1 for details on the vertical profiles). From the vertical soil profiles, it was possible to calculate a volume for each soil layer. The density of the mineral layers was taken from the calculations available at www.pedosphere.com, using a soil texture of 70% sand, 25% silt, and 5% clay. The density of the forest floor was derived from surface soil samples taken in unprepared plots with incubation tubes of known dimensions. By combining the total volume of soil per layer with the density of each layer, a total mass of soil per layer was calculated. Afterwards, N values per soil mass unit were related to total mass of soil per layer to provide a total quantity of N for the whole soil profile. Finally, non-parametric Spearman's rank correlations were conducted between root, stem and soil characteristics for the 45 excavated trees. All statistical analyses used a confidence level of $\alpha = 0.05$ and were conducted using R 2.10.0 (R Development Core Team, 2009).

3.4 Results

3.4.1 Roots – Total numbers

Hybrid poplar tree roots were compared between mounding and unprepared soil through partial excavations of root systems at the base of the trees. Results showed that trees growing

on mounds had a greater total number of proximal roots per tree compared with unprepared plots (respectively 35, SE = 2, and 25, SE = 2, at P = 0.006), but the average root diameter was similar between both treatments (5.1 mm, SE = 0.4, and 4.6 mm, SE = 0.4, at P = 0.4). Differences between treatments were also found among the different root diameter classes. Across the whole soil profile, the number of proximal 0-2 mm diameter roots did not differ between mounds and unprepared plots, whereas the number of proximal roots greater than 2 mm diameter was significantly greater on mounds (Table 3.2).

Table 3.2 Number of proximal roots per tree in mounds and unprepared soil. Numbers from different soil layers and root diameter classes are either combined or not. For mounds, mineral soil layers include the roots from the upper and lower mineral layers. Root numbers are means from 24 (mounding) and 21 (unprepared) excavated hybrid poplars. P-values were produced by mixed analyses of variance comparing mounding with unprepared soil.

	No. roots tree^{-1}	SE	P-value
All soil layers combined			
All root diameter classes			
Mounding	35.0	2.3	0.006
Unprepared	25.5	2.5	
0-2 mm			
Mounding	16.8	1.9	0.25
Unprepared	13.6	2.0	
2-10 mm			
Mounding	12.2	0.9	0.054
Unprepared	9.6	0.9	
11-20 mm			
Mounding	4.9	0.3	<.0001
Unprepared	2.0	0.3	
21-30 mm			
Mounding	0.96	0.2	0.001
Unprepared	0.095	0.2	
In the mineral layers			
All root diameter classes			
Mounding	20.3	2.1	0.25
Unprepared	18.2	2.1	
0-2 mm			
Mounding	7.7	2.0	0.72
Unprepared	8.9	1.7	
2-10 mm			
Mounding	8.5	0.9	0.95

Unprepared	7.8	1.0	
11-20 mm			
Mounding	3.3	0.4	0.0028
Unprepared	1.5	0.2	
21-30 mm			
Mounding	0.83	0.2	0.0049
Unprepared	0	0	
In the forest floor			
All root diameter classes			
Mounding	14.0	1.9	0.037
Unprepared	8.8	2.2	
0-2 mm			
Mounding	8.4	1.5	0.15
Unprepared	5.1	1.6	
2-10 mm			
Mounding	4.3	0.9	0.41
Unprepared	3.1	1	
11-20 mm			
Mounding	1.3	0.2	0.006
Unprepared	0.5	0.2	
21-30 mm			
Mounding	0.04	0.1	0.48
Unprepared	0.14	0.1	

The most striking difference between the two soil preparation treatments was highlighted by the distribution of root diameter classes between soil layers (Table 3.2 and Figure 3.2). It must be noted that in Figure 3.2 and 3.3., depths and thickness of soil layers are based on measurements made of the vertical soil profile during root excavations (to which the soil analyses, described in a following section, broadly correspond). Most importantly, the distribution of 0-2 mm diameter roots among the forest floor and the mineral soil of a given soil preparation treatment, strongly differed between the two treatments. Within the buried forest floor of mounds, the 0-2 mm diameter class was the most abundant of all diameter classes (Figure 3.2). The 0-2 mm diameter roots in mounds were found in equal abundance between the forest floor and the mineral soil, when combining both the upper and lower mineral soil layers, i.e., over and under the buried forest floor (Figure 3.2). In unprepared soils, proximal 0-2 mm roots (as well as all other root diameter classes but the largest, 21-30

mm) were found in greater number in the mineral layer than in the forest floor. When considering the three distinct layers of the mound separately, 0-2 mm roots were more abundant in the buried forest floor (16-23 cm depth) than in both the upper (0-16 cm) and lower (23-31 cm) mineral soil layers (Figure 3.2). The total number of 0-2 mm roots in mounds was significantly greater in the forest floor compared with the lower mineral soil layer. However, the numbers of proximal roots in the 0-2 and 2-10 mm diameter classes were similar between the buried forest floor of mounds and that of unprepared soil, as well as between the combined mineral soil of mounds and the unprepared mineral layer (Table 3.2).

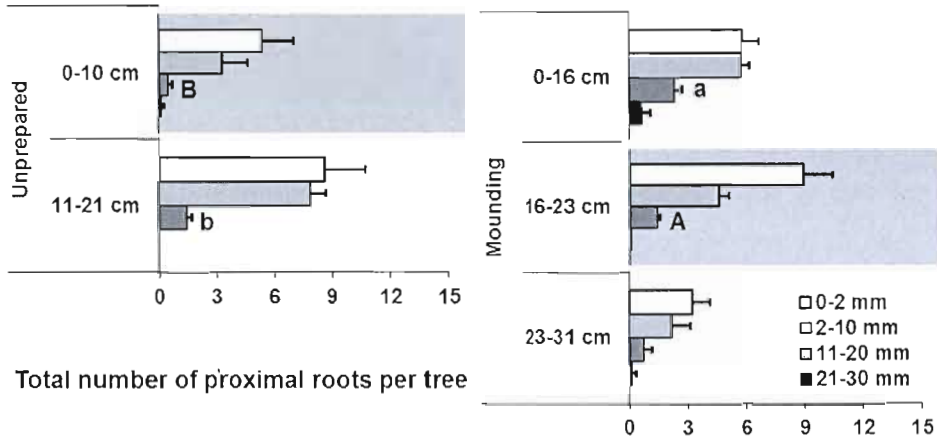

Figure 3.2 Total number of hybrid poplar proximal roots per tree, among four root diameter classes (mm), and for different soil depths that represent soil layers (forest floor emphasized by the shaded area) of the mounding and unprepared treatments. Roots were excavated in a 30-cm radius around the base of the tree. Values are means across eight sites and error bars are SE. Depth and thickness of soil layers are based on measurements made of the vertical soil profile during root excavations. Different letters indicate a significant difference (at α = 0.05) in values between treatments within a given layer of similar soil material (capital letters: unprepared forest floor *vs* buried forest floor; lower case letters: unprepared mineral *vs* mineral soil of mound). Non-significant differences are not shown.

The three distinct soil layers of mounds differed in the number of roots per diameter class. The 0-2 and 2-10 mm diameter classes showed the greatest total numbers per tree within the upper and lower mineral soil of mounds (Figure 3.2). Roots greater than 2 mm in diameter were significantly more abundant in the (combined) mineral soil of mounds compared with

the buried forest floor. The 2-10 and 11-20 mm root diameter classes were more abundant in the upper mineral layer, marginally less in the buried forest floor and significantly less in the lower mineral soil. The largest roots (21-30 mm) were significantly more abundant in the upper mineral soil, and in similar numbers in the buried forest floor and lower mineral layers (Figure 3.2).

3.4.2 Roots – Numbers per unit soil depth

Hybrid poplar roots were further analyzed using numbers of proximal roots per cm of soil depth, which represented a measurement of root density per soil layer (Figure 3.3). The differences between soil layers for the unprepared soils remained the same as when considering the absolute number of roots (cf. Figure 3.2). In mounds, 0-2 mm diameter roots were still most abundant in the buried forest floor, but the relative abundance per cm of soil depth was significantly and greatly higher in this layer than in both the upper and lower mineral layers (Figure 3.3). The proportional abundance of 0-2 mm roots in the buried organic layer of mounds was significantly higher than in the forest floor of unprepared soils, while 2-10 mm roots were marginally ($P = 0.06$) more abundant per cm of soil depth in the buried forest floor of mounds compared with unprepared soils. 0-2 mm roots in the mineral layer of unprepared soils were proportionally more abundant than in the upper mineral layer of mounds, while 2-10 mm roots were proportionally more abundant in the mineral layer of unprepared soils than in both the upper and lower mineral layers of mounds (Figure 3.3). Contrary to the absolute root number figures, the relative abundance of 2-10 mm roots in mounds was higher in the buried forest floor than in the upper mineral layer (instead of being lower). For 11-20 mm roots, the relative abundance was similar between the two mineral layers of mounds (instead of being higher in the upper mineral). Differences between the two treatments remained similar but were more significant.

3.4.3 Roots – Ingrowth cores

Root growth, as represented by biomass of ingrowth cores, varied among soil and vegetation control (VC) treatments (Table 3.3). The two soil treatments, which represented two extremes

in terms of tree growth and intensity of soil disturbance, were marginally different (P = 0.068). Root biomass of ingrowth cores was thus slightly lower in mounded plots (negative estimate, Table 3.3). Vegetation control during the first 3 years resulted in similar ingrowth core root biomass compared with the absence of VC (P = 0.098).

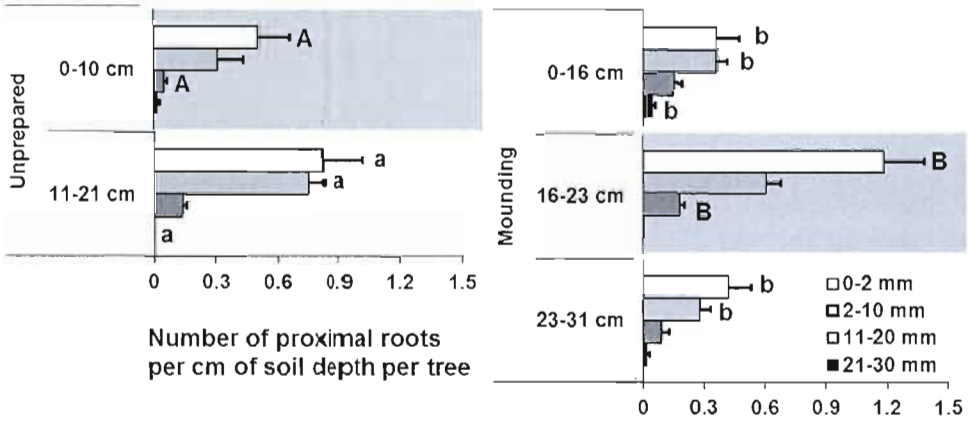

Figure 3.3 Relative number of hybrid poplar proximal roots per cm of soil depth per tree, among four root diameter classes (mm), and for different soil depths that represent soil layers (forest floor emphasized by the shaded area) of the mounding and unprepared treatments. Roots were excavated in a 30-cm radius around the base of the tree. Values are means across eight sites and error bars are SE. Depth and thickness of soil layers are based on measurements made of the vertical soil profile during root excavations (although exact depths may differ). Different letters indicate a significant difference (at $\alpha = 0.05$) in values between treatments within a given layer of similar soil material (capital letters: unprepared forest floor vs buried forest floor; lower case letters: unprepared mineral vs mineral soil of mound). Non-significant differences are not shown.

3.4.4 Soil nitrogen

The ion-exchange resins installed at three different soil depths provided comparison between soil treatments regarding inorganic soil N availability, i.e., $[NH_4+NO_3]$-N (Figure 3.4 a). At depths of 0-5 cm and ~20 cm, significantly higher values were found in the unprepared plots, more than two-fold the values observed in the mounds. Within a given treatment, N concentrations did not differ between depths, with the exception of mounding where

Table 3.3 Results of a mixed analysis of variance comparing root growth across two soil treatments (mounding and unprepared) and two competition level treatments (weeded = aboveground competing vegetation removed during the first 3 years; unweeded = competing vegetation never removed). Root growth was represented by dried root mass retrieved from root ingrowth cores installed at the base of hybrid poplars over one growing season. Roots were not separated by species.

Treatments compared	Dry weight (g) ± SE	Estimate	SE	df	*t*-value	P-value
Mechanical soil preparation						
Mounding	0.824 ± 0.08					
vs Unprepared	1.049 ± 0.09	-0.1833	0.0998	194	-1.836	0.068
Vegetation control						
Weeded	1.010 ± 0.08	0.1618	0.0806	194	2.006	0.098
vs Unweeded	0.810 ± 0.09					

significantly higher concentrations were observed at the ~30 cm depth. This depth was not sampled in the unprepared plots.The values of potential net N mineralization were derived from the *in situ* incubations (Figure 3.4 b). At 0-15 cm, the two soil treatments did not differ in net mineralized N over the 6-week period. At ~20 cm, net mineralized N was significantly higher in mounds compared with unprepared plots. In unprepared plots, net mineralized N was significantly higher at 0-15 cm compared with ~20 cm. Conversely, in mounds, there was no significant difference in net mineralized N between 0-15 cm and ~20 cm, while it decreased significantly at ~30 cm. The calculation of total levels of net mineralized N in the soil rooting volume (Figure 3.4 c) revealed that the buried forest floor of mounds contained significantly less mineralized N than the upper mineral layer because of the difference in thickness and volume of these two layers (Table 3.1).

3.4.5 Above- *vs* belowground growth

The average total tree height in mounds (273 cm, SE = 18) was significantly greater ($P < 0.0001$) than in unprepared plots (171 cm, SE = 17). Diameter at mid-breast height (mid-DBH) showed a similar difference (mound = 27.8 mm, SE = 3.7; unprepared = 14.7 mm, SE = 1.6; $P < 0.0001$). Estimated height: root ratio was significantly higher in unprepared plots than in mounds (mound = 1.5, SE = 0.3; unprepared = 2.7, SE = 0.3; $P = 0.015$). Correlations

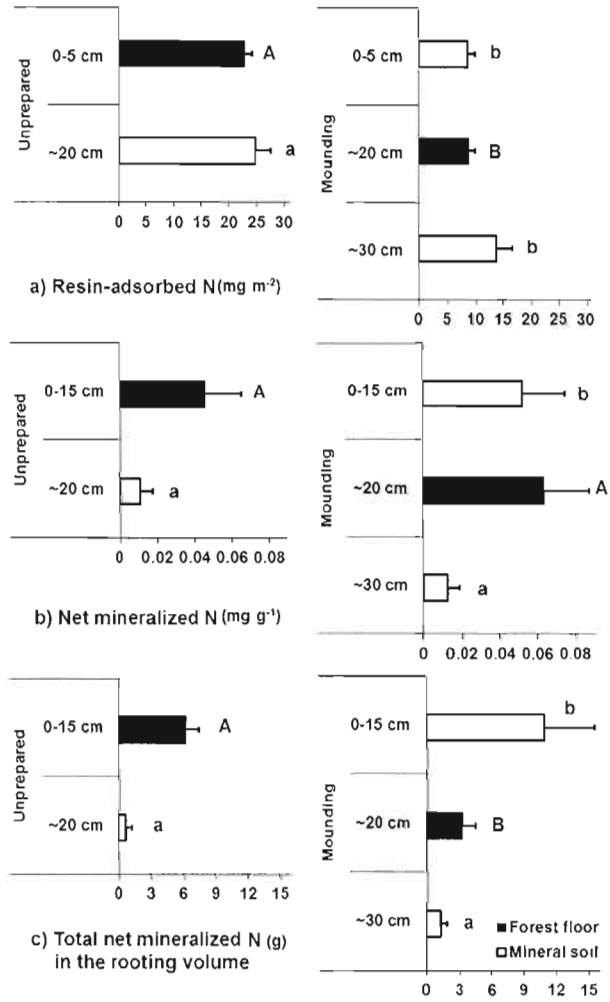

Figure 3.4 a) Concentrations (mg m^{-2}) of total inorganic N, i.e., $[NH_4+NO_3]$-N, adsorbed onto ion-exchange resins buried *in situ* for 6 weeks in the mounding treatment and the unprepared control at different soil depths (0-5 cm, ~20 cm, and ~30 cm for mounds only). b) Net mineralized N (per soil unit mass, mg g^{-1}) upon a 6-week *in situ* incubation of different soil layers at different soil depths for the mounding treatment and the unprepared control. c) Total net mineralized N (g) in the rooting volume, estimated for a cylindrical soil volume of fixed surface area (a circle of 50-cm radius around the tree) and a depth determined by the position in the soil profile of the deepest proximal roots at 3 years of age, which varied between the two treatments (depth and thickness of soil layers are based on measurements made of the vertical soil profile during root excavations). Values are means across eight sites (forest floor, black bars; mineral soil, white bars) and error bars are SE. Different letters indicate a significant difference (at $\alpha = 0.05$) between treatments within a given layer of similar soil material, even though depth and thickness may differ (capital letters: unprepared forest floor *vs* buried forest floor; lower case letters: unprepared mineral *vs* mineral soil of mound).

between root, stem and soil characteristics were constructed for the 45 excavated trees (Table 3.4). Total number of proximal roots per tree was significantly correlated to the stem characteristics of tree height and mid-DBH. Tree height was also a strong determinant of the number of roots in all diameter classes. Mid-DBH was positively correlated to the number of roots in diameter classes, although the coefficients were greater for larger diameter roots (11-20 and 21-30 mm). Only these larger roots were significantly, and positively, correlated to soil temperature. Soil N characteristics did not correlate significantly to root variables. The two smaller root classes (0-2 and 2-10 mm) showed their strongest positive correlations to the total number of roots per tree. The average root diameter per tree was significantly correlated to the number of roots in the 2-10 mm diameter class (Table 3.4). The height: root ratio (tree height over the product of average root diameter and total number of roots) was not correlated to any variable (data not shown).

3.5 Discussion

3.5.1 Root growth in different soil layers

The sampling design used in this study provided information on root distribution and exploration in various soil layers and preferential use of different soil material types within the tree's immediate soil environment (30-cm radius around the base of the tree). It confirmed a previous study (Messier et al. 2009) showing that roots of fast-growing hybrid poplars exhibit a net avoidance of live roots of competing species. This was suggested here by the greater number of proximal roots per cm of soil depth produced in the buried forest floor of mounds compared with the surface forest floor of unprepared soils, despite the fact that the buried forest floor showed a lower resin-absorbed N and a lower total net mineralized N in the rooting volume (Fig. 3.3 b and c). The ratio of root production relative to net N mineralization was thus much greater for hybrid poplars planted in mounds. This implies that hybrid poplar roots avoided the most fertile soil layer when it was already occupied by live roots from other species.

Table 3.4 Correlations on rank (Spearman's rho, ρ) between root characteristics and other soil and tree variables. Mid-DBH is diameter at breast height taken 65 cm above the ground.

Variable 1	Variable 2	Spearman's Rho	Prob>|Rho|
No. of proximal roots per tree	Mid-DBH	0.4862	0.0007
	Total tree height	0.5598	<.0001
Average proximal root diameter per tree	Total tree height	0.1799	0.2371
	Mid-DBH	0.2318	0.1255
	Soil temperature	0.1043	0.4952
No. of proximal roots in diameter class			
0-2 mm	Total tree height	0.3591	0.0154
	No. of proximal roots per tree	0.8548	<.0001
2-10 mm	Mid-DBH	0.3006	0.0448
	Average proximal root diameter per tree	0.3161	0.0344
	Total tree height	0.3723	0.0118
	No. of proximal roots per tree	0.6934	<.0001
11-20 mm	Mid-DBH	0.771	<.0001
	Total tree height	0.68	<.0001
	Soil temperature	0.7881	<.0001
21-30 mm	Mid-DBH	0.6605	<.0001
	Total tree height	0.6333	<.0001
	Soil temperature	0.5405	0.0001

The present study also revealed enhanced colonization of the whole soil environment by hybrid poplar roots in mounds. The warmer and less compacted soil of mounds (Bilodeau-Gauthier *et al.*, 2011) likely provided advantageous conditions for root development. The mounding process also possibly modified the physicochemical conditions of the buried forest floor due to the compaction of the organic matter (of usually low density and large pore size), therefore improving the soil water holding capacity and the soil aeration. These modifications, in turn, might have stimulated microbial activity and favored mineralization of organic matter (see next section on soil nitrogen). A further advantage of the mound might

have been to favour greater adventitious root formation, which is known to frequently occur in *Populus* species (Stettler *et al.*, 1996). Indeed, because of the looser soil of mounds, poplar cuttings may have been planted slightly deeper than in unprepared soils; consequently, a greater portion of the stem would have been in contact with the soil and might have produced a larger number of adventitious roots.

Compared with trees planted in unprepared soils, trees on mounds produced a greater number of proximal roots, particularly larger roots. It is important to note that a proximal root branches into several additional, smaller roots. Hence, larger proximal roots are indicative of a more extensive root system. This was shown in the study by Domenicano et al. (2011) who related proximal root diameter to total root biomass. Finer proximal roots (0-2 mm) in the present study were found overall in equivalent numbers in mounds and unprepared soils. However, in mounds, they were mainly located in the buried forest floor. This layer was assumed to be mostly devoid of live roots from competing species since these were buried and presumably killed during mound formation. The buried forest floor of mounds was also actively explored by larger roots (2-10 and 11-20 mm). In contrast, hybrid poplar roots in all diameter classes partly avoided the forest floor of unprepared soils, which was located at the surface and occupied by numerous living competitor roots. Similarly, at a natural forest site in Sweden, Persson and Stadenberg (2010) found the majority of fine roots of Norway spruce (*Picea abies*) in the top 10 cm of the mineral soil horizon, while the surface organic horizon was mostly colonized by roots of herbaceous plant species.

Greater fine root biomass of hybrid poplars in the absence of root competition was also reported by Messier et al. (2009a) in a split-root pot experiment, where half of the pot was occupied by competing herbaceous species while the other half was bare. The hybrid poplar used in that study (*Populus deltoides x Populus balsamifera*) responded to resource (nutrients) and non-resource (space) belowground competition by avoiding areas of soil with live roots from other species. Competition avoidance was well described by Novoplansky (2009) and Friend (2000). Also, Platt et al. (2004) observed positive shoot response from mountain beech (*Nothofagus solandri*) seedlings after root competition removal, either with or without fertilizer additions, but no response from fertilization alone. This again suggests

that belowground competition for nutrients can be strong and that trees benefit from highly fertile patches the most when competition is low (Kabba *et al.*, 2007). In another area of Quebec, Canada, hybrid poplar plantations also established on formerly forested sites were subjected to different vegetation control treatments (Coll *et al.*, 2007). Controlling vegetation with herbicides was the overall best method, while mechanically removing aboveground plant parts had almost no effect. The authors concluded that vegetation control through herbicide application probably facilitated tree establishment by reducing belowground competition (Coll *et al.*, 2007). In fact, the study by Messier et al. (2009a) suggests that early-successional tree species exhibit avoidance of root competition while late-successional tree species are rather geared toward tolerance of root competition. The authors explained that these mechanisms probably arose through natural selection as ways to improve belowground resource uptake. Early successional trees that do not tolerate competition for light require optimal placement of fine roots in order to maximize resource uptake and fuel their fast and aggressive early growth, hence, root expansion in soil areas free of competing roots and avoidance of areas where competitors are present. On the other hand, late-successional trees establish in already-occupied soil, and therefore must have evolved towards the tolerance of belowground competition (Messier *et al.*, 2009a).

3.5.2 Soil nitrogen

The amounts of soil NH_4 and NO_3 adsorbed to ion-exchange resins suggested that the soil N supply in unprepared soils was more than two-fold that in mounds, for all soil layers. Nitrogen availability as measured by ion-exchange resins basically represents the amounts available in the soil solution in the resin's vicinity, and should be one of the most important factors influencing root distribution in the soil profile (Hangs *et al.*, 2004). Based only on these nutrient availability observations, one would have expected tree growth to be lower on mounds compared with unprepared soils. This was not the case.

Values from ion-exchange resins are affected by many microsite conditions. First, the ions absorbed by plant roots cannot be captured by the resin membrane. As hybrid poplar trees on mounds developed a larger biomass and a much larger root system than on unprepared soils,

they may have been more efficient at absorbing available forms of N. However, there were more roots from competing species in the control plots compared with the mounds, although this did not appear to reduce the amounts of N captured by resins in the control plots. Second, as inorganic N was mostly present in NH_4 form in these acidic soils (mean of NH_4 on total N in incubation data = 83%, SD = 21), tree N uptake would be mostly through diffusion more than through mass flow. Because ion-exchange resins are dependent on mass flow to bring ions in adsorption range, they may therefore underestimate the amount of N available to plants (mean of NH_4 on total N in resin data = 62%, SD = 19). Hence, despite the low N values of ion-exchange resins in mounds, the amounts of this nutrient available to trees might not necessarily be lower than in unprepared soil.

The amount of N in mounds being equivalent to that in unprepared soils is further supported by the N mineralization measurements from incubation tubes. Yet, studies have shown that increased tree growth and, in turn, increased N uptake may lead to substantial decreases in extractable or soil solution NO_3 and NH_4 (Bélanger *et al.*, 2004, for Populus grandidentata Michx.; Bernhard-Reversat, 1996, for Eucalyptus spp.; Moukoumi *et al.*, submitted for publication, for Salix spp.). Even though the mineral soil in the upper part of mounds was poorer in total and resin-adsorbed N than was the surface forest floor of the unprepared soils, absolute net N mineralization values were not different. These measurements indicate that the disturbed soil conditions induced by mounding were just as adequate as those of undisturbed soil to promote the release of N to tree roots via mineralization. As exposed in the previous section, the physicochemical conditions induced to the forest floor by the mounding process may have been beneficial to the microbial activity, therefore favoring N mineralization.

A previous study done at the same sites showed that mounds had lower total C and N concentrations in the surface soil, while an absence of MSP resulted in soils that were richer in these elements (Bilodeau-Gauthier *et al.*, 2011). If one were to compare net N mineralization (from incubation tubes) with total N concentrations, N mineralization at the surface of mounds would represent a strikingly large part of total soil N, over 22%, whereas it would remain at 2 to 3% in unprepared soils. Faster mineralization is important for tree

nutrition during a given stand rotation, although it also raises the question of whether it could lead to long-term depletion of nutrient reserves (Örlander *et al.*, 1996).

Because the upper mineral layer of mounds occupies a large volume, its relatively high N mineralization rates translated into greater total amounts of net mineralized N than in undisturbed soils. It suggests that the upper mineral soil is the greatest contributor to available N in mounds, while in the undisturbed soils it is the forest floor. In addition, the assessment of N by ion-exchange resins revealed, for both soil treatments, that amounts of N were highest in the mineral layer located below the forest floor, despite its lower N mineralization rates. It suggests that the forest floor, whether it is buried or not, contributes to enriching the underlying mineral soil with N.

While the unprepared soils in the present study experienced a decrease in net N mineralization with depth, it remained similar between the surface mineral horizon and the buried forest floor of mounds. The upturning of mineral soil to create the mound resulted in warmer and less compacted soil (Bilodeau-Gauthier *et al.*, 2011), which is typical of mounding (Örlander *et al.*, 1990 ; Sutton, 1993). The increased temperature in mounds probably generated favourable conditions for the decomposition of forest floor material and mineralization of N, by increasing the activity of microorganisms that transform organic N into mineral forms available for plant root uptake (Leirós *et al.*, 1999). Also pointing to possibly favourable conditions of N mineralization is the increase of available N (as registered by PRS^{TM}-probes) in the lowest soil layers of mounds. This could reflect mineralized and newly available N from the buried forest floor that would have leached down the soil profile. Hodge (2003) hinted at a similar phenomenon in a study on spatially heterogeneous soil N supply.

3.5.3 Soil disturbance creates hot spots for tree nutrition

The mounding process induces soil disturbance by modifying the vertical arrangement of soil layers, notably by burying the forest floor under a quantity of mineral soil. This burial has both the advantage of favouring soil N dynamics and of greatly reducing root competition for

resources. Given that the buried forest floor of mounds represented a lower proportion of the whole vertical soil profile than did the surface forest floor of unprepared soils, the preference of proximal roots for this buried layer, as demonstrated by the high abundance per cm of soil depth, is particularly persuasive in regard to the nutritional advantage provided by mounding. It has been shown that the vertical distribution of fine roots may influence the outcome of competition between species, for instance by increasing the level of competition when species exhibit a similar root distribution (Bauhus et Messier, 1999b ; Bauhus *et al.*, 2000). Species that are sensitive to root competition would therefore tend to avoid such a situation. This response to competition appears important in the explanation of the advanced colonization by fine roots of the buried forest floor in mounds compared with the surface organic horizon of unprepared soils. Thus, even though unprepared soils are richer in nutrients than mounds, they probably contain more live roots of competing species, and pioneer tree species such as *Populus* generally avoid competition.

3.5.4 Hybrid poplar yield

Contrary to expectations, the height: root ratio (i.e., tree height divided by the product of average root diameter and total number of roots) was lower for the faster-growing hybrid poplars planted on mounds compared with those in unprepared soils. These results do not concur with previous work suggesting that smaller (or slower-growing) plants normally allocate more biomass to roots to obtain limiting nutrients (Cahill, 2003 ; Tiainen *et al.*, 2006). Even though trees on mounds exhibited a smaller value for the height: root ratio compared with unprepared plots (see the Results section), root colonization by trees growing on mounds did not proceed at the expense of stem growth. Indeed, the trees on mounds were actually taller than those in unprepared plots, and tree height was strongly and positively correlated to the expansion of the root system. Consequently, a low height: root ratio proxy was in that case a benefit to the overall growth of the trees. It suggests that a larger root system, which provided access to more available resources and resulted in greater nutrient uptake, actually increased aboveground growth of hybrid poplars. Coyle and Coleman (2005) demonstrated that increased stem biomass in *Populus* clones did not result from a simple shift in biomass allocation from roots to shoot. They showed that shoot: root biomass ratios of

clones did not vary between fertilized and unfertilized trees, even though other plant species are known to change their shoot: root ratios in response to N availability (Ågren et Franklin, 2003 ; Beck, 1996). In addition, belowground competition for space was presumably high in unprepared soils, as root biomass from ingrowth cores was slightly higher in unprepared soils compared to mounds. Therefore, the smaller root system and higher height: root ratio of trees growing in unprepared soils could very well result from avoidance of the already densely populated surface forest floor. Another limiting factor for root growth could have been the lower temperature of unprepared soils compared with mounds (Bilodeau-Gauthier *et al.*, 2011).

When planted in favourable conditions, juvenile hybrid poplars can easily outgrow other woody species and thus efficiently acquire light. However, newly planted trees often face harsh competition from herbaceous species, notably grasses, whose negative effect stems mainly from belowground competition (Collet *et al.*, 2006). As such, early soil treatments such as soil mounding are very efficient for these species, which then require less control of the competing vegetation in subsequent years. It is nevertheless conceivable that slower-growing species would respond differently to such management strategies. For instance, Boateng et al. (2009) showed that spruce, which in the absence of silvicultural treatments was physically overtopped by vegetation, benefited more from lasting reductions in tall shrub and aspen abundance (i.e., increased light availability) than from early effects of mechanical soil preparation on the rooting microsite. Nevertheless, Cortini and Comeau (2008) observed that although 11 to 13-year-old white spruce were affected by surrounding woody shrubs in competition for light, herbaceous plants also had a detrimental impact on the growth of these trees via root competition, because of the spruces' shallow root system that put them in direct contact with herbaceous plant roots.

3.6 Conclusion

Mounds provided several nutritional and environmental advantages over unprepared soils. Firstly (1), by burying the forest floor, the mounding process severely reduced the competing vegetation, thus decreasing the competition for soil nutrients and making them available for

poplar uptake, as well as freeing the space within this nutrient-rich layer for hybrid poplar roots to explore. Secondly (2), the upper mineral layer of mounds showed relatively high N mineralization rates despite lower total organic matter and total N content compared with the surface forest floor of unprepared soils. Thirdly (3), the loose and warm soil conditions typical of mounds favoured root production and elongation, which in turn allowed hybrid poplar roots to access a larger soil volume and a greater nutrient pool. Fourthly (4), this extra biomass allocation to roots on mounds was immediately rewarded in terms of greater N uptake, which could have either increased photosynthetic rates (and the overall growth of trees on mounds) or eliminated the former N limitation.

This research has confirmed that the roots of fast-growing hybrid poplars, and likely other pioneer trees, exhibit avoidance of competition for soil resources. It has also provided insights and increased our understanding of optimal root proliferation in regard to different vertical arrangements of soil horizons and soil resources in the presence of competition. The reported response of hybrid poplar trees to these conditions will be important to consider in future management of the soil substrate in tree plantations under intensive silviculture. Soil management that aims at inducing a vertical rearrangement of soil layers in tree plantations may thus be an alternative to more labour-intensive, time-consuming, or potentially environmentally-damaging vegetation control methods, such as high levels of herbicide or mechanical methods involving intensive top soil displacements. It may also improve access to soil resources and optimize aboveground growth for fast-growing pioneer trees.

3.7 Acknowledgements

This study was funded by the "Fonds québécois de recherche sur la nature et les technologies" through a research grant to C. Messier et al. (project #2007-FO-118127), as well as a Ph.D. scholarship to S. Bilodeau-Gauthier. The authors acknowledge the essential participation of Louisiana-Pacific Corp., Chambord, QC division, notably C. Lavoie and M. Bonneau, in lending land and personnel for tree planting, machinery for soil preparation, and overall for their openness to our testing. Other instrumental partners were the "Ministère des Ressources naturelles et de la Faune du Québec" (MRNFQ; particularly P. Périnet and A.

Fauchon for advice regarding poplar clones) and the Quebec Intensive Silviculture Network (RLQ; P. Gagné and B. Bigué for their contribution and coordination of the project). Early contributors to setting up the project also include D. Cormier (FERIC), W.H. Hendershot (McGill University), P. Périnet (MRNFQ), and G. Prégent (MRNFQ). Western Ag Innovations (Saskatoon, SK, Canada) generously provided a discount on PRS^{TM}-probe analyses. Field work was made possible thanks to the help of P. Gagné, L. St-Antoine (CFS), A. Beaumont, S. Reynolds, and A. Turgeon.

CHAPITRE III

SPATIAL DISTRIBUTION OF SOIL NUTRIENTS MODIFIES THE BEHAVIOUR OF HYBRID POPLAR ROOTS IN COMPETITION WITH GRASSES

4.1 Abstract

Root plasticity in response to soil heterogeneity is crucial to ensure efficient foraging for soil resources by plants. Root plasticity can provide a competitive advantage in heterogeneous environments. The objective of this study was to assess the response of hybrid poplar roots to the presence of competition by grasses (*Calamagrostis canadensis*) with different spatial distributions of soil nutrients (homogeneous or heterogeneous). An outdoor experiment was set up using large soil-filled pots in which slow-release fertilizers were incorporated, either uniformly throughout or concentrated in one half of the pot occupied by either a hybrid poplar or a grass tuft. Analysis of root morphology and architecture revealed that hybrid poplars mostly avoided the soil areas where the competing grass was planted. This avoidance was less pronounced when the competitor's pot half was richer in nutrients than the poplar's pot half. A richer poplar pot half always led to less poplar root expansion and smaller poplar shoot growth. Spatial heterogeneity of soil nutrients can thus be a boon or a curse to the hybrid poplar, depending on how soil nutrients are distributed in its immediate vicinity. It shows that the spatial distribution of soil nutrients can modify the behaviour of hybrid poplar roots facing competing grasses, to the extent of influencing the outcome of competition.

Key words : *Calamagrostis*, hybrid poplar, plant competition, root plasticity, spatial nutrient distribution.

4.2 Introduction

Biomass allocation to roots, as well as root morphology and architecture, are influenced by the supply of soil resources (Hodge *et al.*, 2009 ; Karban, 2008) and by plant competition (Hutchings *et al.*, 2003 ; Novoplansky, 2009). These two factors are, in turn, strongly affected by forest and plantation management operations (Bilodeau-Gauthier *et al.*, in preparation ; Heineman *et al.*, 1999a ; Örlander *et al.*, 1990 ; Sutton, 1993). The development of the root system may have important consequences for the initial survival and establishment of a tree, and for its future development and growth (Burdett *et al.*, 1983 ; Grossnickle, 2005 ; Hibbs *et al.*, 2003 ; McCreary et Duryea, 1987). This study aimed at determining how the spatial distribution of the soil nutrient supply, combined with the presence or absence of competition, can impact the development, morphology, and architecture of hybrid poplar roots in soil–plant mesocosms.

Root growth plasticity in response to enriched soil patches (George *et al.*, 1997 ; Hodge, 2006) may optimize root expansion and promote efficient foraging for resources in heterogeneous soils (Hodge, 2004). It could contribute to improving the productivity of forest trees and be particularly significant to the success of tree plantations (Friend *et al.*, 1999). It appears very relevant considering that spatial heterogeneity is widespread in natural ecosystems worldwide (Kohlpaintner *et al.*, 2009 ; Okin *et al.*, 2008 ; Rodríguez *et al.*, 2009) and that both spatial and temporal heterogeneity (Kelly, 2008) are important factors in explaining the coexistence of species (Pacala et Tilman, 1994 ; Tilman, 1982 ; Tilman et Pacala, 1993). Optimal root foraging (McNickle et Cahill, 2009 ; McNickle *et al.*, 2009) could benefit natural and planted forests that deliver essential ecosystem services (Byrne et Milne, 2006 ; Paquette et Messier, 2010) as well as plantations of fast-growing trees that may provide for future lumber and energy needs (Christersson, 2010 ; Johansson et Karačić, in press ; Paris *et al.*, 2011).

But how do roots develop in response to soil heterogeneity? According to Hutchings and John (2004), plant responses to environmental heterogeneity are not always predictable from patterns observed under homogeneous conditions, yet these responses can have important

effects on resource allocation and plant growth. Plant roots have a number of strategies at their disposal for nutrient acquisition in heterogeneous environments (Hodge, 2009 ; Hodge *et al.*, 2009), and various root foraging traits in response to soil heterogeneity have been identified (Rajaniemi, 2007 ; Zhang *et al.*, 2010). Heterogeneous soil conditions can induce plastic responses in plant root distribution and architecture (Bauhus et Messier, 1999b ; Campbell *et al.*, 2002 ; Casper *et al.*, 2003), in the allocation of biomass between above- and belowground parts, as well as in total plant yield (Hutchings *et al.*, 2003).

Plasticity was shown to be of vital importance in resource acquisition by plants (De Kroon *et al.*, 2009 ; Grime, 1994 ; Grime et Mackey, 2002). Morphological characteristics of roots can be altered by trees, either at the level of the individual root or that of the whole root system (Leuschner *et al.*, 2004). Localized proliferation of roots in a nutrient-enriched soil patch accompanied by reduced root growth outside that patch is a common phenomenon (Pregitzer, 2008). Producing thinner roots that present a larger specific root surface area (SRA, surface area per unit mass) increases the surface area of the root system for the same investment in carbon, thus improving the cost/benefit ratio of root production. Such plasticity in SRA may as well improve the water and nutrient uptake per unit mass of root when area-related uptake rates are constant (Tyree *et al.*, 1998). Root architecture can exhibit substantial plasticity in response to the surrounding soil conditions, notably the nutrient supply (Drew *et al.*, 1973 ; Fitter *et al.*, 1991 ; Grime *et al.*, 1986). Hutchings et al. (2003) reported in a review that a high density of roots within nutrient-rich soil patches had been observed in both laboratory and field experiments. Yet, as suggested by earlier studies (Passioura et Wetselaar, 1972 ; Wetselaar *et al.*, 1972) and confirmed by a later review (Robinson, 1994), increased proliferation in rich soil patches is far from being universal among plant species, with one third of the species reviewed by Robinson (1994) not responding to rich patches.

Competition could be higher in soils with rich patches compared with more homogeneous soils given the same overall nutrient supply, according to a review by Hutchings et al. (2003). Consequently, patterns of nutrient supply would influence inter- and intraspecific plant interactions. Caldwell et al. (1996) similarly showed important interactions between species within nutrient-enriched soil patches. Root plasticity can confer a strong competitive ability

in heterogeneous environments (Craine, 2006 ; Fransen *et al.*, 2001 ; Hodge *et al.*, 1999). For instance, several studies have described the competitive advantage resulting from plasticity in the production of lateral root branches (De Kroon et Mommer, 2006 ; Hodge, 2006 ; Kembel et Cahill, 2005 ; Kembel *et al.*, 2008). Roots of certain plant species tend to proliferate in response to belowground competition. Bartelheimer et al. (2006) called "aggregation strategy" the situation where plants produce more roots in the presence of competition and, above all, in the very area where competing roots are found. The better competitor whose roots proliferate first into a fertile soil patch may well acquire all available nutrients before inferior competitors have the opportunity, as in the theory of "supply pre-emption" (Barley, 1970 ; Comerford *et al.*, 1994 ; Craine *et al.*, 2005). In contrast, Schenk et al. (1999) demonstrated how roots of certain species or in certain conditions may be "territorial" and keep to soil areas where no competitors are present, what they referred to as spatial segregation. Plastic root responses to nutrient-rich soil microsites and to competition for resources figured among the factors causing segregation. This question of root segregation is akin to discussions around root avoidance patterns (Messier *et al.*, 2009a). Day et al. (2003b) showed how the spatial pattern of soil nutrient distribution could alter the competition levels in a plant community, thus affecting plant growth, survival, as well as community structure.

The objective of this study was to test the response of hybrid poplars to 1) the presence of competition (*Calamagrostis canadensis* grasses) and to 2) the spatial distribution of soil nutrients (either homogeneously or heterogeneously distributed), as well as 3) to assess the interaction between the response to competition and the spatial distribution of soil nutrients. It was hypothesized that *i*) competition would reduce the above- and belowground development of hybrid poplars, whose roots would avoid soil areas containing competing roots; *ii*) poplar development would benefit from a spatial nutrient distribution that results in greater proximity to available soil nutrients; and *iii*) that poplar root avoidance of competition would be less pronounced when soil nutrients were heterogeneously distributed and concentrated in the competitor's area.

Cahill et al. (2010) undertook an experiment relatively similar to the present one, although they used an annual herbaceous plant, *Abutilon theophrasti*, in assessing the response to the

presence of a competitor and to a heterogeneous resource distribution. Studies on herbaceous plant root response to environmental heterogeneity are much more numerous compared with the few similar studies on tree roots (i.e., Campbell *et al.*, 2002 ; Coleman, 2007 ; van Vuuren *et al.*, 2003). These few studies, however, focused on heterogeneity of soil nutrients and did not extend their observations to the interaction with competition. The present study is therefore the first to assess the response of a tree species to both competition and spatial heterogeneity of soil nutrients. The results should prove important in furthering the knowledge on plant behaviour as well as in designing adequate soil management practices for fast-growing tree plantations.

4.3 Methods

Hybrid poplars were the main focus of this study because they are increasingly planted around the world for pulp, bioenergy, and lumber production purposes (e.g., Christersson, 2008, 2010), as well as for the creation of riparian buffer zones in agricultural areas (Fortier *et al.*, 2010a, 2010b). Moreover, they are generally very sensitive to belowground competition (Bilodeau-Gauthier *et al.*, 2011 ; Kabba *et al.*, 2007 ; Messier *et al.*, 2009a), and a recent field study suggested that the spatial distribution of soil nutrients and the location of competing roots might interact to influence both root and shoot growth (Bilodeau-Gauthier *et al.*, in preparation). *Calamagrostis canadensis* was chosen as the antagonist because it is well recognized as a strong competitor in boreal regions (Landhäusser et Lieffers, 1998 ; Landhäusser *et al.*, 2007 ; Lieffers *et al.*, 1993), particularly for belowground resources. It was thus able to rapidly incite a response in the studied trees, which is important in a short-term experiment.

4.3.1 Experimental design

The study was set up outdoor beneath a 50% light-filtering mesh hung on an overarching structure 3 m above the ground. The mesh created a roof and walls around the structure in order to protect the plants from excessive sun and wind. Below that structure, 72 pots were located at a distance of 30 cm from each other, in which were combined different treatments

of competition (2 levels), spatial nutrient distribution, hereafter shortened to soil fertility (3 levels), and hybrid poplar clones (3 levels), with each combination of treatments replicated in four pots. In the following sections, the three fertility treatments are abbreviated as HETr (heterogeneous soil fertility, with nutrients concentrated on the poplar's pot half, or heterogeneous rich), HETp (heterogeneous soil fertility, with nutrients concentrated on the pot half opposite to the poplar, or heterogeneous poor), and HOM (homogeneous soil fertility). They are followed by an indication of the competition treatment, either "-C" (with competition) or "-noC" (no competition). Figure 4.1 summarizes visually the six combinations of competition × fertility treatments.

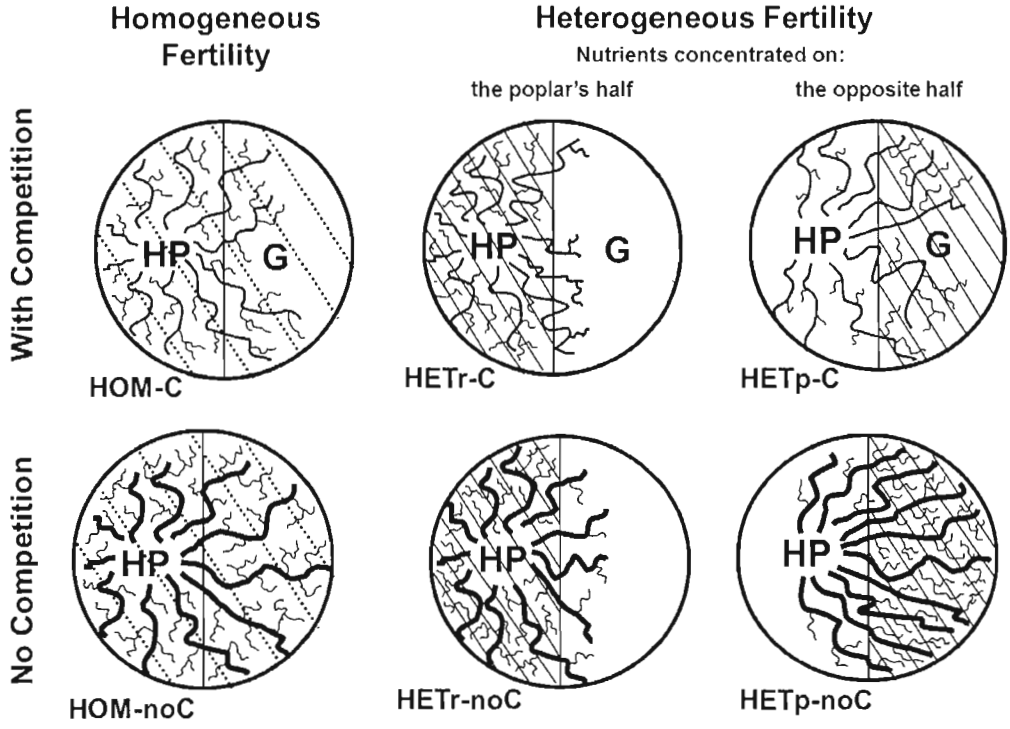

Figure 4.1. Schematic representation of the six combinations of competition (2 levels; rows) × fertility (3 levels; columns) treatments. A hybrid poplar (HP) was planted in one half of the pot, and a *Calamagrostis* grass (G) tuft on the other half. Resulting root systems are conceptually drawn, where thicker lines represent greater root biomass. Heterogeneous treatments may also be thought of as whether the poplar is planted in the richest (HETr) or the poorest (HETp) pot half.

Location of individual pots within the experimental area was randomized. This experiment was conducted at the Laurentian Forestry Centre, a Canadian Forest Service research facility in Quebec City, QC, Canada (46°48′ N, 71°23′ W). An overhead automatic sprinkler irrigation system watered the pots every day for 30 min at 18:00. Three hybrid poplar clones were selected (915319, *P. balsamifera* × *P. maximowiczii*; 3308, *P. deltoides* × *P. nigra*; and 3729, *P. nigra* × *P. maximowiczii*) One the clones was also used in previous field experiments (Bilodeau-Gauthier *et al.*, 2011 ; Bilodeau-Gauthier et al., Bilodeau-Gauthier *et al.*, in preparation), while the other two were clones commonly in use in Quebec; the present experiment included three clones in order to ensure that the observed responses would not be ascribable to a lone clone particularity. Wild-grown patches of the grass *Calamagrostis canadensis* were dug out from a nearby forest clearing next to a countryside road. Each patch was chosen as a group of three to four grass shoots growing close to each other in an area of approximately 150 cm^2; soil was taken along down to 5-10 cm deep, including a good number of belowground *Calamagrostis* rhizomes. A grass patch would thus fit in one to two full hands. Care was taken to eliminate from the patch all plant species other than *Calamagrostis*.

Round pots with a containing capacity of 44 L (30 cm high, inner diameter of 36 cm at the base and 41 cm at the top) were filled with a mechanically-mixed amalgam of peat moss, sand, vermiculite, and Turface® MVP® (Profile Products LLC, Buffalo Grove, IL, USA), in proportions 40:34:13:13. Each pot was virtually separated in two equal halves. In the middle of one half would be planted a hybrid poplar cutting, while the other half would either be left bare ("no competition") or occupied by a patch of *Calamagrostis* ("with competition"). Hybrid poplar cuttings had been kept in dormancy at 4°C until planting (on June 17), four days after which the buds started flushing and the leaves growing. A small amount of fertilizer was added on day 9 to facilitate establishment without enriching the substrate too much (250 mg with the following nutrient content, by weight: 23% total N, 19% P_2O_5, 17% K_2O, 0.5% Mg, 0.12% chelated Fe, 0.05% chelated Zn, 0.05% chelated Mn, 0.05% chelated Cu, 0.02% B, 1% tetrasodium EDTA, 0.005% Mo, and a maximum of 0.3% Cl). The three spatial fertility treatments were set up when most of the poplar cuttings started producing leaves, on day 23 (July 10). Slow-release fertilizer coated granules (Basu *et al.*, 2010) were

disposed at the soil surface, with each pot receiving a total of 30 g of fertilizer granules (content, by weight: 8% total N, 15% P_2O_5, 9% K_2O). Fertility treatments differed in the proportions in which the fertilizer granules were distributed among the two halves of the pot, either equally (50:50%) for the spatially homogeneous fertility treatment, or more concentrated in one pot half (15:85%) for the two spatially heterogeneous fertility treatments (*i*- on the poplars' half of the pot, and *ii*- on the opposite half). On day 55, 21 days after the start of, and halfway into the fertilizer treatment, pots were moved around randomly within the experimental area to eliminate potential border effects.

The experiment was terminated on day 70 (August 26), thus 46 days after fertilizer treatments started, and plants were delicately uprooted by hand. Hybrid poplar height was measured, and aboveground parts were separated from belowground parts. The number of hybrid poplar leaves per pot was calculated. *Calamagrostis* aboveground shoots were counted, their maximum height was measured, and they were kept for chemical analysis. Poplar leaves and grass shoots were oven-dried at 70°C for 48 h and weighed for total mass per pot, before being submitted to the following chemical analyses. Total foliar nitrogen (N) of poplars and grasses was determined on a LECO CNS analyzer (LECO Corporation, St. Joseph, MI, USA). Foliar phosphorus (P) was analyzed, following calcination at 500 °C and dilution with hydrochloric acid (Miller, 1998), by flow injection analysis and ion chromatography (FIA; Lachat Instruments, Milwaukee, WI, USA). Foliar base cations (Ca, K, Mg) were determined by atomic absorption and emission (Varian, model AA240FS, Palo Alto, CA, USA). Three poplar leaves per pot were kept apart to be scanned for leaf area analysis using WinFOLIA (Régent Instruments, Ste-Foy, QC, Canada). Soil samples were taken on a subset of pots in order to verify that fertility treatments had been maintained throughout the whole experiment. These samples were taken in both halves of pots, and in a number of cases also in both the upper and lower portions of pots ($n = 50$).

4.3.2 Root analyses

Hybrid poplar roots that started from the main stem were cut at their base and divided into two groups: 1) those growing towards the poplar's half of the pot, and 2) those growing

towards the other half. This means that the pot volume sampled on the poplar's half of the pot was lower than the opposite pot half. The poplar roots were carefully extracted by hand by following the roots from the tree stem to the root tip, which allowed easily distinguishing and separating them from grass roots. Grass roots were not sampled. Poplar roots were washed carefully so as to maintain the integrity of the root system. They were scanned and analysed with the WinRHIZO software (Regent Instruments, Québec, QC, Canada). Prior to scanning, roots were dyed by immersion in a 0.1% methylene blue solution during 24 h. This darkened the otherwise naturally pale poplar roots and ensured a better image acquisition by the scanner, a technique adapted from Bouma et al. (2000). When the root system of a given tree was too large to scan all at once, it was separated in smaller samples, whose data were subsequently pooled. Root samples were placed in a thin transparent plastic tray covered with a film of water in order to facilitate root positioning and image acquisition.

WinRHIZO is an image analysis system specifically designed for root measurements. It can do morphological, topological (links), architectural (branching), and color analyses. It is comprised of a computer program and image acquisition components adapted for root image acquisition and analyses. However, it needs to be well calibrated and carefully used for optimal measurements (Bauhus et Messier, 1999a). The software calculates root measurements using its own non-statistical measuring method. Morphological measurements include root length, surface area, volume, average diameter, and number of tips, forks, and crossings. The precision of root diameter measurement was set at regular. Image smoothing was set at low, while debris filtering was assigned to discard objects with an area smaller than 0.1 cm^2 or a length: width ratio smaller than 10.

Link analysis was also conducted on root images. The WinRHIZO software calculates the length, diameter, surface area, and number of root links, which are classified as external-external (EE), external-internal (EI), and internal-internal (II). Length, diameter, and surface area were averaged for each link class. This classification is based on seminal work by Fitter (1987), who developed an analytical approach to root architecture called topology, which was a related but distinct outlook on root architecture compared with the previous developmental and morphometric methods (see Fig. 1 from Fitter, 1986). The developmental method (Rose,

1983) attributed a fixed value to a root segment depending on its original appearance within the root system (the "root order"), with the base root as order 0 and with an increasing value for each successive lateral root. A root segment's identity thus never changed from base to tip, even though its ecological and physiological function might as further branching occurred along its axis. The morphometric method (Fitter, 1982b) went the other way around by labelling terminal branches as first-order segments, two of which joined to make an order 2 segment, and two order 2s made an order 3, etc. It has the benefit of allowing for an assessment of the physiological function of individual roots (e.g., by identifying the nutrient-absorbing terminal roots), as well as combining all roots of similar function unto the same order. It also acknowledged that the physiological function of a root segment might change over time.

The topological approach (Fitter, 1985, 1986, 1987) improved upon its predecessors by being based on root links rather than segments (a link is a length of root between two nodes or branching points). When using topology, a given root link is assigned a "magnitude" equal to the number of external (i.e., terminal) links that are connected to it. The whole root system has a magnitude equal to that of the last link (or base link), therefore representing the total number of external links. The root system may also be characterized by its external path length, which is the sum of all links in all classes. Again, a link's identity may change over time, as does the root system's identity. Topology is more informative about physiological functioning of the root system than the morphometric approach, since a single parameter characterizes the entire root system (see also Fitter et Stickland, 1991 ; Fitter *et al.*, 1988 ; Fitter *et al.*, 1991). Fitter (1982a) pioneered the idea that the form (architecture) of root branching is related to its function (acquisition of soil resources), which was confirmed by subsequent research (Hodge *et al.*, 2009 ; Pregitzer, 2008) showing for instance that N uptake is dependent upon root architecture (Liu *et al.*, 2008). Root architecture also bears importance in plant productivity (Lynch, 1995).

In the topological approach, external links are those that terminate in a meristem (i.e., root tips), while internal links are closer to the main branch (See Fig. 1 from Fitter, 1987). Internal link length represents the frequency of branch production once initiated and has an important

influence on the form of root systems (Fitter, 1982a ; Lungley, 1973) and is influenced by availability of soil resources. EE links encompass the external links that stem from other external links; EI links are external links starting from internal links; and II links are internal links that are joined to other internal links. Fitter (1986, 1987) showed that herringbone-like root systems have a high proportion of EI links, and indicated that they are the most efficient at exploring space but the least transport-efficient and the most expensive to produce. Herringbone-like root systems are often encountered in plants grown in resource-limited soils (Glimskär, 2000 ; Taub et Goldberg, 1996). Berntson (1994) proposed that plants would have to strike a balance between exploitation efficiency (volume of soil explored per unit volume of root) and exploitation potential (its extent or scale). Another trade-off commonly discussed is the one between scale and precision of root foraging (Campbell *et al.*, 1991 ; Grime, 2007b); scale and precision might however both be strategies towards the efficiency of foraging (De Kroon et Mommer, 2006).

4.3.3 Hypotheses

Several hypotheses were tested in the present study, and this section expands on the summarized hypotheses presented in the introduction: 1) Competition by *Calamagrostis* grasses will reduce the above- and belowground development of hybrid poplars; specifically, we expect to observe, in the presence of competition, lower tree height, shoot biomass, leaf biomass, and leaf N. 2) Poplars will exhibit avoidance of competition from grass roots; we thus expect to observe, in the opposite pot half (the one with grass), lower poplar root biomass, root length, and root surface compared with the poplar's pot half. 3) In the absence of competition, aboveground poplar production will benefit from a greater proximity to an available nutrient source (i.e., more nutrients on the poplar's pot half), and thus will increase in the order HETp < HOM < HETr. Belowground production (as the ratio of opposite pot half over poplar's pot half) will increase in the order HETr < HOM < HETp. It should be noted that an alternate hypothesis by Lamb et al. (2004), in regard to the annual herbaceous *Abutilon theophrasti*, stated that foraging for fertile patches would result in a larger root system and could lead to more nutrient uptake and greater shoot growth. 4) In the presence of competition, the spatial distribution of nutrients will influence the response to belowground

competition, so that poplar roots will still profilerate, albeit moderately, in the grass's pot half when it contains more nutrients than the poplar's pot half. Specifically, we expect that the ratio of the grass's pot half over the poplar's pot half for root variables will vary in the order: HETr-C < HOM < HETp < HETr. 5) It is usually acknowledged that root systems with proportionally more (or longer) external links are known to be more energy-efficient foragers, while root systems with a great number of external links stemming from internal links (EI links) are particularly inefficient (what Fitter (1987) dubbed "herringbone root systems"). Hence, we expect to observe, in the pot half with fewer nutrients, a higher average external link length, a greater number of external links and fewer internal links, and a higher average root diameter (implying fewer fine roots and thus less nutrient uptake capacity). 6) Ultimately, although trees that are adapted to being in competition with other plants should react to resource competition by being more efficient in their root foraging and investment, competition-intolerant pioneers such as poplars are expected to either be less efficient or show no change.

4.3.4 Statistical analyses

Root data for the two pot halves were built into a ratio of (opposite pot half): (poplar's pot half) for each tree. This implies, for instance, that a tree showing a ratio higher than 1 for root length produced longer roots on the opposite pot half than on its own pot half. However, because the tree was planted in the middle of its pot half, the root system would naturally expand more on the other half, and the pot ratio be higher than 1. Hence, the intent of these analyses was not to determine whether roots were equally separated between the two pot halves. The objective was rather to assess how the pot ratio would vary according to the treatments. To continue with the preceding example, another tree showing an even higher ratio would thus present an even greater difference in root length between the two pot halves than the first tree. This ratio of the two pot halves is indicated hereafter by the expression "pot ratio". Aboveground (and some belowground) variables were considered per the whole pot – and tree ("pot total").

The response of hybrid poplars to the presence of the *Calamagrostis* grass and the spatial distribution of soil nutrients was assessed through a factorial analysis of variance (ANOVA) with competition, soil fertility, and clone type as categorical fixed effects. Normality and homoscedasticity of data were verified with the Shapiro-Wilk and Bartlett's tests, respectively. When necessary, ln transformations were applied to the variables that did not satisfy to preceding tests. Lastly, to facilitate the multiple comparisons of treatments and the presentation of results, the three clones were considered as one, and the competition and fertility factors were combined into a single factor, "treatment", divided into six levels (2 from competition × 3 from fertility) for use in one-way ANOVAs.

The maintenance of the fertility treatments was verified by submitting soil nutrient data to matched pairs t-tests between values of the two pot halves and between values of the upper and lower portions of pots. In all cases, the spatial distribution of nutrients was adequately maintained between the two pot halves and no excessive leaching of nutrients to the bottom of pots occurred throughout the course of the experiment. All statistical analyses were conducted on R 2.12.1 using significance levels of 0.05 and 0.1.

4.4 Results

The root systems of hybrid poplars grown in the six combinations of competition × spatial nutrient distribution treatments are conceptually schematized in Figure 4.1.

4.4.1 Root morphology and architecture

Total root biomass of hybrid poplars, when computed as the pot total, was significantly reduced in the presence of competition compared with no competition (Fig. 4.2 a). However, it did not differ according to fertility treatments. Similarly, the major morphological and architectural root variables usually reported in the scientific literature (e.g., length, specific root length, surface area, branching events, termination numbers), when taken as the pot total, were reduced by competition but remained unaffected by fertility treatments (data not

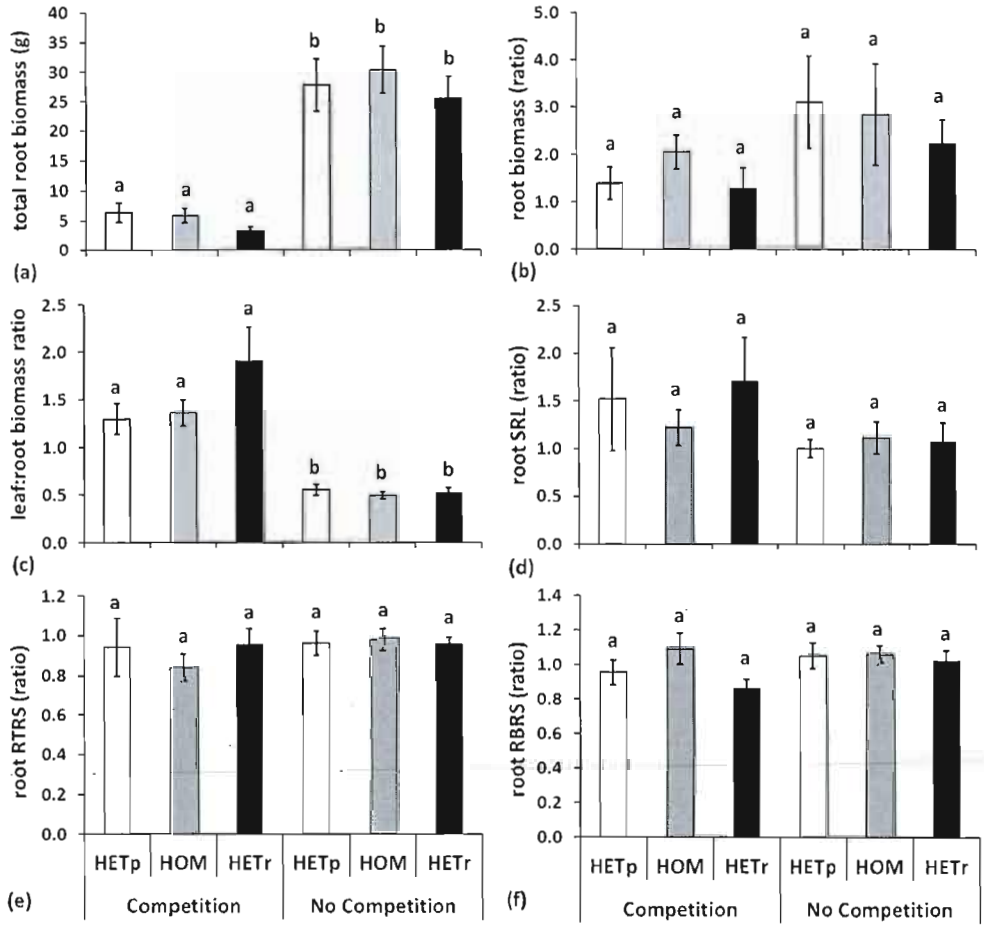

Figure 4.2. Root morphology and architecture of hybrid poplars per the six combined fertility × competition treatments. From left to right within a competition treatment, the treatments are placed in increasing order of nutrient content on the tree's pot half. HO = homogeneous fertility (grey bars); HE = heterogeneous fertility, with the tree planted in the poorest pot half (white bars); HEP = heterogeneous fertility, with the tree planted in the richest pot half (black bars); w = with competition; wo = without competition. Values are means from 12 pot replicates, error bars are SE. Different letters indicate significantly different means (at P = 0.05; results of one-way ANOVAs and post-hoc Tukey's HSD tests). SRL: specific root length (root mass over root length). RTRS: root termination number over root surface. RBRS: root branching events over root surface. Units indicated in brackets as "ratio" indicate that values were computed as the ratio of the poplar roots that explored the pot side opposite to the tree over those that remained on the tree's own pot side.

shown). Yet, the treatments HETr-C and HETp-noC differed in regard to the pot total of the specific root length (respectively 2.37 and 4.14 mg cm^{-2}, at $P = 0.1$).

The ratio of root biomass between the two pot halves, i.e., the spatial distribution of root biomass within the pot, was not significantly different between the six treatments (Fig. 4.2 b), even though the tendency of the response to the presence of competition was similar to that of the pot total. Both competition and nutrient treatments had no significant effect on the pot ratios of basic architectural variables such as of specific root length (SRL, root mass divided by root length, Fig. 4.2 d), root termination number over root surface (RTRS, Fig. 4.2 e), and root branching events over root surface (RBRS, Fig. 4.2 f). The treatments HETr-C and HETp-noC differed in regard to the pot ratio of root length (ratios of 1.03 and 3.35, respectively, at $P = 0.09$).

4.4.2 Root links

All link analyses presented here were done on the ratio of poplar roots found on the pot half opposite to the poplar over the roots found in the pot half occupied by the poplar (hereafter called "pot ratio") rather than on the pot total, because the aim was to assess spatial differences in root architecture (specifically, topology) in response to treatments that induced spatial differences in the environment. In addition, pot totals of root link data usually responded similarly to the total root biomass (data not shown), i.e., more roots meant more links, thus not providing further insights.

Overall, characteristics of root links showed significant differences between certain treatments, with some that emphasize the response to competition and others that indicate a response to the spatial nutrient distribution (Fig. 4.3). The treatment with a heterogeneous distribution of nutrients concentrated in the poplar's pot half (heterogeneous rich) and with the presence of competition, abbreviated as HETr-C, was often different from one, or more, of the other treatments, particularly the ones with a homogeneous distribution of nutrients with or without competition (HOM-C and HOM-noC).

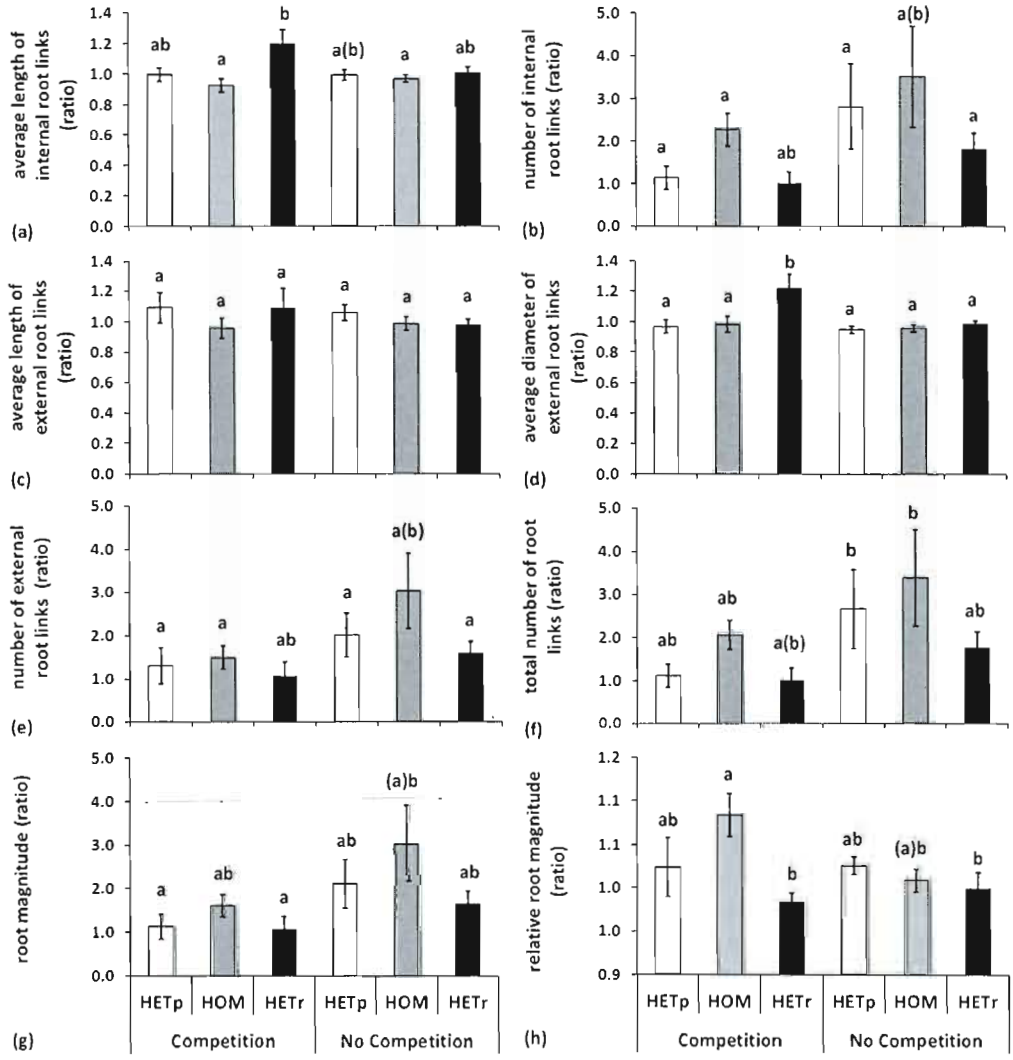

Figure 4.3. Link analysis of hybrid poplar roots per the six combined fertility × competition treatments. From left to right within a competition treatment, the treatments are placed in increasing order of nutrient content in the tree's pot half. HOM = homogeneous fertility; HETp = heterogeneous fertility, with the tree planted in the poorest pot half; HETr = heterogeneous fertility, with the tree planted in the richest pot half. Values are means from 12 pot replicates, error bars are SE. Different letters indicate significantly different means (at P = 0.05 for normal letters or at P = 0.1 for letters in brackets; results of one-way ANOVAs and post-hoc Tukey's HSD tests). Units indicated as "ratio" denote that values were computed as the ratio of the roots that explored the pot side opposite to the tree over those that remained on the tree's own pot side. Root magnitude = number of external links (both external-external and external-internal links); relative root magnitude = number of external links over the total number of links.

The pot ratio of the length of internal root links of hybrid poplars was significantly higher for the HETr-C treatment compared with the HOM-C and HOM-noC treatments (Fig. 4.3 a). The pot ratio of the number of internal root links was significantly lower for the HETr-C than for the HOM-noC treatment (Fig. 4.3 b). External link length did not differ between treatments (external-external links, EE, Fig. 4.3 c; external-internal links, EI, P = 0.50, data not shown). Average diameter of external links showed a significantly higher pot ratio in the HETr-C treatment compared with all others (Fig. 4.3 d). The pot ratio of the number of external root links was higher for HOM-noC than for HETr-C (Fig. 4.3 e). The total number of root links – called external path length by some authors – tended to have a higher pot ratio for trees growing in the absence of competition, but the differences were only significant for the HETr-C treatment compared with HETp-noC and HOM-noC (Fig. 4.3 f). Magnitude of the root system, i.e., the number of all external root links (EE + EI), presented a pot ratio that was higher for the HOM-noC treatment compared with HETp-C and HETr-C (Fig. 4.3 g). The relative root magnitude, calculated as the proportion of external links (EE + EI) over the total number of links, had a higher pot ratio in the HOM-C treatment compared with the HETr-C, HETr-noC, and HOM-noC treatments (Fig. 4.3 h). The pot ratio of the number of EI root links (i.e., external links that are connected to internal links) followed the exact same pattern as the root magnitude (data not shown).

4.4.3 Aboveground growth and leaf characteristics

Aboveground variables of hybrid poplars mainly differed according to competition levels (Fig. 4.4). Poplars growing in the presence of *Calamagrostis* showed lower shoot height and biomass (Fig. 4.4 a-b), higher ratio of leaf biomass to root biomass (Fig. 4.2 c), lower total leaf biomass (Fig. 4.4 d), lower total tree biomass (shoot + root; i.e., Fig 4.4 b + Fig. 4.2 a), lower leaf N concentrations (Fig. 4.4 e), and lower total leaf N content in a tree (Fig. 4.4 f). Specific leaf weight (Fig. 4.4 c) and foliar content of other nutrients (P, K, Ca, and Mg; data shown in Appendix) did not vary between competition treatments. All aboveground variables remained similar between fertility treatments. Yet, there was a tendency for hybrid poplar height to decrease from homogeneous to heterogeneous nutrient distribution, with lowest heights for nutrient heterogeneity concentrated on the poplar side (Fig. 4.4 a).

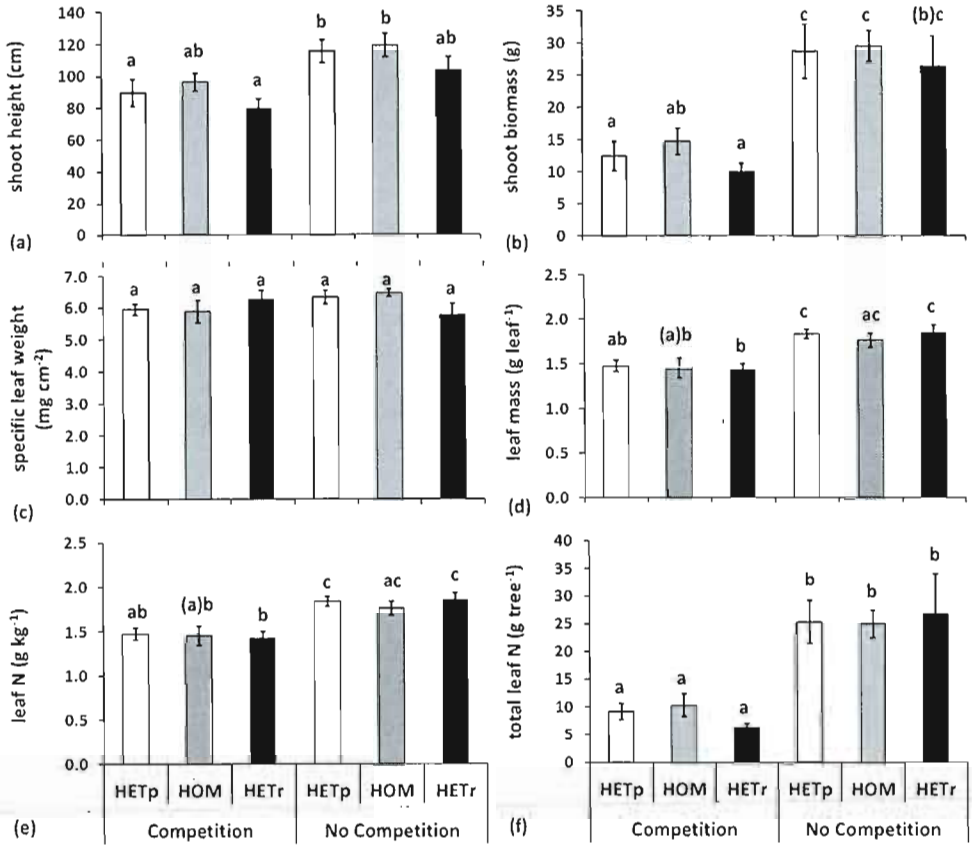

Figure 4.4. Aboveground growth and leaf morphology of hybrid poplars per the six combined fertility × competition treatments. From left to right within a competition treatment, the treatments are placed in increasing order of soil nutrient content in the tree's pot half. HOM = homogeneous fertility; HETp = heterogeneous fertility, with the tree planted in the poorest pot half; HETr = heterogeneous fertility, with the tree planted in the richest pot half. Values are means from 12 pot replicates, error bars are SE. Different letters indicate significantly different means (at P = 0.05 for normal letters or at P = 0.1 for letters in brackets; results of one-way ANOVAs and post-hoc Tukey's HSD tests).

4.4.4 Clones

The three poplar clones showed some differences in aboveground variables (data shown in Appendix), i.e., shorter height but greater number of shoots and higher leaf N content for the 3308 clone; greater leaf and shoot biomass for the 3729; greatest specific leaf weight (g cm^{-2})

for the 3729 and lowest for the 915319; leaf Ca and Mg concentrations decreasing in the order 915319 > 3308 > 3729. Total root biomass, total root length, and total specific root length increased between clones in the order 915319 < 3308 < 3729, while the shoot: root biomass ratio followed the opposite trend. However, clones showed no differences in regard to most other root variables. Furthermore, the factorial analysis of variance revealed that clone type had very few significant interactions with the competition and fertility treatments, and the general response to the latter two treatments was the same for all clones (data not shown).

4.4.5 Calamagrostis

The grass *Calamagrostis canadensis* responded to neither competition nor fertility treatments in terms of variables such as maximum shoot height, number of shoots, and total shoot biomass. Grass shoot contents of N, P, and K were significantly higher in the heterogeneous soil nutrient distribution treatment with nutrients concentrated on the grass side, while grass shoot contents of Ca, Mg, and Mn did not differ between fertility treatments (data shown in Appendix). Grass roots were not measured, but visual observation at the time of pot sampling indicated that they had explored the totality of the pot, no matter the fertility treatment, and did not seem to respond to fertility treatments. This implies that the level of competition that hybrid poplars faced in the treatment with "presence of competition" would not vary when combined with the different fertility treatments.

4.5 Discussion

The present study confirmed that growing in the presence of competition from *Calamagrostis* grasses greatly reduced hybrid poplar development, both above- and belowground. It also showed that poplar roots were sensitive to the spatial distribution of nutrients by proliferating more in soil areas with a greater nutrient supply. Moreover, it was revealed that the outcome of belowground competition was influenced by the spatial distribution of soil nutrients, and that it contributed to the resulting aboveground growth.

4.5.1 Response to the spatial nutrient distribution

The response of poplar roots to soil areas of higher nutrient availability was emphasized by the following root characteristics and comparisons of treatments (also listed in Table 1): 1) the pot ratio of internal link length in the HETr-C treatment, which was higher than in the HOM-C, HOM-noC, and HETp-noC treatments (Fig. 4.3 a); 2) the pot ratio of the average diameter of external links, which was higher for HETr-C compared with all other treatments (Fig. 4.3 d); 3) the relative root magnitude (pot ratio of the number of external links (both EE and EI) over the total number of links), which was higher for HOM-C compared with HETr-C and HETr-noC (Fig. 4.3 h). These characteristics are what Berntson (1994) articulated as 'size-independent aspects' of root architecture. As they were the most responsive to the treatments, it suggests that the plastic adaptation to environmental conditions shown by hybrid poplars was expressed through rather subtle modifications of the root system. Alternatively, root architecture might be the first to adapt to these conditions, while morphology would eventually show modifications in a longer-term experiment. Yet, the poplar root response might have been more explicit given total nutrient levels in pots lower than those used in this study.

The higher pot ratio of the internal link length observed in the HETr-C treatment means that when soil nutrients were concentrated on the poplar's pot half, internal links of roots growing towards the opposite side were longer (Fig. 4.3 a). Internal link length was described by Fitter (1987) as the frequency of branch production once initiated and identified as an important influence on the form of root systems. In the HETr-C treatment, branching into external links was less frequent in the opposite pot half, possibly because the conditions encountered by the foraging roots there (i.e., presence of competition, lower nutrient availability) made soil exploration less appealing.

External links, as stated in the Methods section, are those ending with a root meristem. As such, they might be compared to root hairs or fine roots, which are usually defined by their diameter (commonly < 2 mm, although more conservative assessments restrict fine roots to diameters < 1 mm). These fine roots are considered to be the most active in regard to water

and nutrient uptake from the soil (Danjon et Reubens, 2008 ; Grotz et Guerinot, 2002 ; Zewdie *et al.*, 2008). The production of new root links is considered to be indicative of root proliferation. Gross et al. (1993) studied four herbaceous species that showed significant increases in root numbers and root length in fertilized patches. This root proliferation in fertilized patches was largely due to increased birth (i.e., branching) rates of new roots. New root links may sometimes be produced in response to a low nutrient supply, as shown by Williamson et al. (2001). They exposed how lateral root growth of *Arabidopsis* was responsive to phosphate availability in soils, favouring the production of lateral (external) over primary (internal) roots when soil P was low. Root proliferation thus appears to be relevant for nutrient uptake even though mycorrhizal connections are also known to be important for the acquisition of slowly-diffused elements such as P.

As mentioned above, the opposite pot half of the HETr-C treatment presented an intrinsically low nutrient content combined with the presence of competition that further reduced nutrient availability. Yet, the two treatments (HOM-C and HOM-noC) that differed from HETr-C comprised both competition levels (with and without), which suggests that their higher production frequency of new external links in the opposite pot half was mainly due to the fertility treatment. Specifically, it implies that the homogeneous nutrient distribution created attractive fertility conditions that made root exploration in farther soil areas worthwhile, regardless of whether they were already occupied or not by competing roots.

The average length and diameter of external links over those of internal links between each pot half (Fig. 4.3 c-d) shone out as the most different in the treatment HETr-C. The pot ratio of the external: internal link length for HETr-C was the lowest (significantly different from the HOM-C treatment), while its diameter ratio was the highest (significantly different from all treatments but HETr-noC). This implies that a tree growing in a highly fertile initial environment and in the presence of competition produced, in its immediate vicinity, external root links that were longer and thinner (i.e., possibly better at nutrient uptake) than internal links compared with the opposite pot half, where nutrients were fewer and competition was stronger. In those soil areas farther away from its starting position, both the scarcity of

resources and their depletion by competing roots resulted in shorter and thicker roots that produced fewer external links, and where root foraging was thus less effective.

The pot ratio of the average length of external links (both external-external and external-internal links) did not differ between treatments. Fitter (1987) reported for *Trifolium pratense* that the length of external root links, representing the distance behind the apex at which branching occurred, was reduced by NO_3^- ions. This meant that a root system could produce shorter external links in soil areas where NO_3 was more available to achieve the same uptake. If there had been a similar phenomenon in the present study, the pot ratio of external link length would have been lower in treatments where soil fertility (and thus, NO_3 content) was higher on the pot half opposite to the poplar. Fitter (1987) also showed that the average length of external-internal root links of the herbaceous species *Trifolium pratense* decreased significantly at higher soil P concentrations, but remained similar at varying N concentrations. Here, both N and P soil concentrations varied between treatments but hybrid poplars did not respond in the same manner as *T. pratense*, perhaps because root architecture of trees reacts differently to environmental conditions compared with that of herbaceous plants.

The present results are comparable overall to the three previous studies that looked at tree root response to soil heterogeneity (Campbell *et al.*, 2002 ; Coleman, 2007 ; van Vuuren *et al.*, 2003). Campbell et al. (2002) created heterogeneous conditions within root ingrowth-cores and reported that black spruce (*Picea mariana* Mill.) fine roots selectively proliferated within the richer soil zones. Coleman (2007) showed that the response of four tree species from southeastern USA to spatial heterogeneity of soil resources occurred at the level of the whole root system, with both fine and coarse roots proliferating in enriched soil patches, rather than being simply a feeder root response. Van Vuuren et al. (2003) compared responses to soil heterogeneity between seedlings of two temperate hardwood tree species, red maple (*Acer rubrum* L.) and gray birch (*Betula populifolia* Marsh.). They used the split-root method (where a tree's root system was split between two pots) and simulated soil heterogeneity by adding organic matter and nutrients in only one of the two pots. Gray birch, a species which appears much earlier in forest succession compared with red maple, showed

greater plasticity in response to the heterogeneous soil treatment, with increased root biomass, specific root length, and N uptake in the enriched pot.

The response of plant roots to resource heterogeneity may vary among species due to different overall foraging strategies, as shown by the different conclusions reached by previous studies. Ryel and Caldwell (1998) modelled the nutrient uptake of the desert herbaceous plant *Agropyron desertorum* in relation to the spatial distribution of soil nutrients. They suggested that root uptake of NO_3 and PO_4 was greatest for a homogeneous distribution of nutrients, and that root uptake of NO_3 was reduced by a heterogeneous distribution more than was the uptake of PO_4. On the other hand, species accustomed to arid conditions are not particularly fast-growing and may thus lack the plastic capability to respond to spatial heterogeneity of soil nutrients. Day et al. (2003a) showed the benefits of heterogeneity by submitting the herbaceous plant *Cardamine hirsuta* to different treatments of spatially heterogeneous soil fertility, which resulted in greater root, shoot, and total biomass, as well as lower mortality (Day *et al.*, 2003b), for the individuals in the heterogeneous compared to the homogeneous treatment. Hodge (2003) reported that soil N uptake by two herbaceous plant species was greater when organic matter (OM) was homogeneously distributed rather than concentrated in patches. This was attributed to a faster release of N from OM into the soil solution under homogeneous conditions, due to a larger surface accessible for OM decomposition by microbial organisms. On the contrary, Graciano et al. (2009) showed that a spatially localized distribution of fertilizers (i.e., heterogeneous) was preferable for *Eucalyptus grandis* to one where fertilizers were thoroughly mixed (i.e., homogeneous). The *Eucalyptus* seedlings produced more root biomass in the PO_4-fertilized soil patch, while total root biomass in the pot did not change. The authors concluded that the heterogeneous distribution treatment was possibly more favourable because it reduced immobilization of P in the soil and thus maintained its availability for root uptake. They also observed reduced N uptake for trees grown in the homogeneous treatment, which resulted from their more limited exploration of the soil substrate compared with trees in the heterogeneous treatment.

4.5.2 Response to competition

The present study showed that hybrid poplarss were negatively affected by competition, particularly belowground, in agreement with previous studies (Bilodeau-Gauthier *et al.*, in preparation ; Kabba *et al.*, 2007 ; Messier *et al.*, 2009a). Since specific leaf weight (Fig. 4.4 c) remained similar across treatments, it indicates that there was no modification in the type of leaves (either shade or light leaves) produced by the trees. Hence, competition for light was not an important factor in this study and all differences in aboveground parts between competition treatments were due to belowground competition.

The negative effects of competition manifested when poplar roots actively avoided soil areas that contained competing roots. Competition had a limiting effect on poplar development that was particularly noticeable on total root biomass, which was reduced about five-fold for trees undergoing competition. Shoot biomass was also affected by competition, but was only reduced two- to three-fold in the presence of competition. Root response to competition is listed below and will be explained in details thereafter.

The restriction of root foraging induced by the presence of competition was most emphasized by the following root characteristics (also listed in Table 4.1) encountered in treatments with presence of competition: 1) lower total root biomass (Fig. 4.2 a); 2) lower leaf: root biomass ratio (Fig. 4.2 c); 3) generally lower pot ratio of the number of root links of all types (Fig. 4.3 f); 4) less frequent production of external root links (i.e., longer internal root links of HETr-C compared with HETp-noC and HOM-noC, Fig. 4.3 a, and lower number of internal links in HETr-C than in HOM-noC, Fig. 4.3 b); and 5) lower total N content in the foliage of a tree, which indicates a lower uptake of soil N by roots (Fig. 4.4 f). The ratio of root biomass between the two pot halves, however, did not seem to be affected by competition levels (Fig. 4.2 b), as is often observed in species exhibiting competition avoidance (cf. Messier *et al.*, 2009a). The large data variability from the poplars growing without competition might have affected the response.

The present results relate more to the root segregation (Schenk *et al.*, 1999) than to the root aggregation theory (Bartelheimer *et al.*, 2006). The latter states that plants tend to overproduce roots in response to non-self conspecific competition. However, this root aggregation may be more present in annual and perennial herbaceous species than in trees, because trees grow and develop over a long timeframe in the presence of other plants. As a result, they may react differently to non-self root competition than the much shorter-lived herbaceous species. Root segregation (Schenk *et al.*, 1999), on the other hand, is synonymous with the term "avoidance" used by other authors (Messier *et al.*, 2009a) and favoured in the present study.

4.5.3 Interaction between competition and spatial nutrient distribution

Despite the aforementioned impacts of competition on root development, poplar roots still proliferated in the fertile soil areas even though that implied closer contact with the competing grass (Table 4.1). This was emphasized by (1) a topological characteristic here called the relative root magnitude, which is the proportional number of external links over the total number of links (Fig. 4.3 h). As these external links are considered to fulfill the role of nutrient uptake, their number relative to other links is probably representative of root exploration and foraging. Relative root magnitude had a higher pot ratio for HOM-C than for HETr-noC. This indicates that trees growing in the presence of competition and in the homogeneous fertility treatment exhibited greater foraging and exploration patterns compared with trees that grew without competition in the heterogeneous treatment with nutrients concentrated on the poplar's side. Moreover, (2) the strong root foraging that occurred despite the presence of competition also suggests an ability of hybrid poplar roots for plasticity. Indeed, the relative root magnitude in the soil area occupied by competing roots observed in the HOM-C was also higher than the one in the HOM-noC treatment. This suggests that given similar conditions of spatial nutrient distribution, a hybrid poplar can plastically adapt to the presence of competition by producing a higher proportion of external root links, even though its absolute root biomass is lower.

Therefore, homogeneously distributed soil nutrients for which there was no competition led to a greater exploration of space that was not restricted by production costs (possibly a sign of a herringbone root system). This was probably due, in the HOM-noC treatment, to *i*) a greater return on the investment (nutrient acquired per C devoted to root growth) for roots produced in the opposite half, and *ii*) to an initial nutrient reservoir sufficiently large to fuel the expansion of the root system.

Overall, the present results are in agreement with Messier et al. (2009a), although root avoidance and the nuancing effect from enriched soil manifested differently. These authors conducted a split-root pot experiment where half of the pot was occupied by competing grasses while the other was bare. They reported greater fine root biomass of a hybrid poplar clone (*Populus deltoides* × *P. balsamifera*) in soil areas devoid of root competition. On the contrary, strong patterns of competition avoidance were revealed by morphological (specific root length) and architectural (branching) root characteristics, as roots of poplar trees grew significantly less in soil areas that contained competing roots. Yet, hybrid poplars still produced roots in soil areas of high root competition that received fertilizer additions, albeit in lower numbers and mainly of fine roots.

The present results are relatively similar to the conclusions of an experiment by Cahill et al. (2010) on the annual herbaceous plant *Abutilon theophrasti*. They observed that root systems of plants grown alone expanded into the entire pot no matter if soil resource distribution were homogeneous or heterogeneous. In the present study, trees indeed expanded greatly in the absence of competition, but they showed a slight preference for soil areas with higher nutrient concentrations. *A. theophrasti* growing in the presence of competitors and in homogeneous conditions of resource distribution showed a greatly reduced root system, as well as spatial segregation of the soil substrate between competitors. This reduction of the root system in response to competition was more modest when the spatial nutrient distribution was heterogeneous. In the present study, trees in both the homogeneous and heterogeneous (but concentrated on the opposite pot half) nutrient distributions resulted in tree roots foraging nonetheless in the competitor's vicinity. This slight divergence between the two studies may be due to the actual nutrient concentration levels, the difference in nutrient concentration

between the fertile patch and the rest of the soil substrate, as well as the nutrient requirements of the species. Overall, the present study agrees with Cahill et al.'s (2010) suggestion that plants may possess the ability to modify their behaviour by integrating information about their environment, in this case competing neighbours and the spatial distribution of soil resources (cf. Cahill, 2011 regarding plant "behaviour"; Karban, 2008 ; McNickle *et al.*, 2009).

4.5.4 Influence of the belowground response on the aboveground response

The initial fertility conditions, i.e., the nutrient supply in the pot half where the tree was planted, influenced the outcome of competition. Hybrid poplar shoot height and biomass were seemingly determined both by initially available soil nutrients and by the nutrient potential of the distant soil area later explored by roots. More precisely, aboveground growth appeared to be favoured by a compromise between initial and later nutrient resources. Indeed, an initial nutrient supply of intermediate levels (in the present case, the nutrient concentrations found in the homogeneous treatment), coupled to an equivalent amount in the soil area explored later on, turned out to be the best condition for aboveground hybrid poplar growth. This is indicated by the fact that poplars in the homogeneous fertility treatment with presence of competition (HOM-C) exhibited: 1) greater root foraging behaviour (Fig. 4.3 a-d-h) and 2) were the only ones, among the treatments with competition, that showed height and biomass values that were not different from those of trees growing without competition (Fig. 4.2 a-b).

Benefiting from a good starting position, i.e., being planted in the richest pot half, thus proved important as long as it did not limit soil exploration and expansion of the root system. Otherwise, the root system of a tree could found itself confined to an overall smaller soil volume. This was indicated by the case of hybrid poplar trees planted in highly fertile soil conditions (heterogeneous rich, HETr), which resulted in these trees not exploring as far in the distant soil areas as did other trees whose initial soil conditions were less favourable (heterogeneous poor, HETp; or homogeneous, HOM). Instead of acting as an early boost to the expansion of the root system, a fertile local soil prompted tree roots to focus their

foraging effort in their starting area, as it was probably the most cost-effective in regard to nutrient foraging. On the contrary, trees for which initial fertility conditions were not better or were worse than conditions in distant soil areas were required to develop more extensive root systems and forage further (and farther) in order to acquire the same amount of resources than trees planted in the richer pot half. This extensive foraging probably led these trees to have access to an overall greater supply of soil resources, which translated into greater production of aboveground biomass. Trees in homogeneous fertility conditions developed better than those in heterogeneous conditions starting in the poorer half of the pot, probably because the latter had fewer initial resources on which to capitalize in order to promote root expansion and soil exploration.

4.5.5 Considerations for plantation and forest management

In the pot experiment undertaken in the present study, trees with greater root expansion and foraging into a larger soil area exhibited better aboveground development. The importance of a large soil volume was also shown in a recent field experiment with hybrid poplars, which indicated that a low nutrient availability per soil unit mass could be compensated by accessing a large nutrient reservoir (Bilodeau-Gauthier *et al.*, in preparation). Both the field study and the present pot experiment agree with previous studies, for instance that of Aerts et al. (1991), who showed, in a competition experiment on shrubs and grasses, that competitive ability depended strongly on the plasticity of spatial root development and on the production of an extensive root system covering a large soil volume.

Soil heterogeneity requires a certain level of plasticity on the part of tree roots for their growth, development and exploration of the soil environment in order to ensure optimal root placement and resource uptake. The soil disturbance that results from mechanical soil preparation (MSP) methods often used in tree plantations can also induce heterogeneity in soil conditions. For instance, the mounding treatment commonly used in Scandinavia and Canada (Örlander *et al.*, 1990 ; Sutton, 1993), and recently tested in hybrid poplar plantations (Bilodeau-Gauthier *et al.*, 2011, in preparation), modifies the original vertical arrangement of soil layers in important ways. While the original soil profile consists of only two main layers

– a forest floor layer over a mineral soil layer –, a mound presents three layers, i.e., an overturned mineral layer at the surface, a buried forest floor, and a lower mineral layer. It was showed that hybrid poplars can benefit from this heterogeneity-inducing MSP (Bilodeau-Gauthier *et al.*, in preparation). Notably, a high abundance of hybrid poplar fine roots was reported within the buried organic layer, which was rich in nutrients but mostly devoid of competing roots, possibly indicating developmental root plasticity. That field study used only one clone, and other clones or cultivars could have responded differently to these soil conditions, as belowground allocation was indeed shown to vary across genetic gradients in *Populus* species (Fischer *et al.*, 2007). However, the present study showed that three different hybrid poplar clones submitted to competition and spatial nutrient distribution treatments responded in similar ways, although to possibly different extents.

4.6 Conclusion

Hybrid poplar roots responded to the presence or absence of belowground competition and to the spatial distribution of soil nutrients. Competition was uniformly detrimental to total root and shoot biomass of poplars. It also resulted in much lower N uptake, as revealed by total content in the foliage. The spatial distribution of soil nutrients influenced the extent of root expansion, as poplars whose initial soil surrounding was nutrient-richer than the rest of the pot showed limited root proliferation and soil exploration. On the contrary, trees planted in equivalent or nutrient-poorer conditions compared with the distant soil areas tended to explore and forage to a greater extent. This was emphasized by size-independent characteristics of root architecture. As a general rule, poplars developed better when there was both *i*) an initial nutrient supply that was sufficient to fuel expansion of the root system and *ii*) an attractive nutrient supply in distant soil areas that made root foraging worthwhile. Hence, the homogeneous nutrient distribution was in the present case a worthy compromise. It allowed a hybrid poplar to benefit from a larger soil volume through extensive soil exploration, thus probably granting access to a greater nutrient reservoir that resulted in superior aboveground development. Most importantly, the spatial nutrient distribution interacted with the competition level to modify the outcome of competition. This was emphasized by the similarity in shoot and root development between a) trees growing in the

absence of competition under a spatially heterogeneous nutrient supply concentrated in their immediate vicinity (HETr-noC) and b) trees growing in the presence of competition under a spatially homogeneous nutrient supply (HOM-C).

4.7 Acknowledgements

This study was funded by the "Fonds québécois de recherche sur la nature et les technologies" through a research grant to C. Messier et al. (project #2007-FO-118127), as well as a Ph.D. scholarship to S. Bilodeau-Gauthier. The experimental design benefited from the facilities made available at the Laurentian Forestry Centre (Canadian Forest Service [CFS], Natural Resources Canada) in Quebec City, QC. The authors are grateful for the collaboration of the Quebec Intensive Silviculture Network (RLQ; notably P. Gagné) and the Ministère des Ressources naturelles et de la Faune du Québec (MRNFQ; particularly P. Périnet and A. Fauchon) for providing the poplar cuttings and for advice on growing hybrid poplars in pots. Field work was made possible thanks to the help of several people at the CFS: L. St-Antoine, É. Pelletier, K. Gommier, and J. Laganière. Information on where to find wild *Calamagrostis* grasses was generously provided by G. Ayotte (Université Laval). The authors also acknowledge the hospitality of F. Berninger's lab (UQAM) where the root scans were undertaken.

CONCLUSION

Cette thèse a permis de clarifier les besoins du peuplier hybride durant son développement juvénile, en identifiant les conditions environnementales requises pour assurer sa survie initiale et promouvoir sa croissance subséquente en sol forestier boréal. De plus, cette recherche a expliqué le comportement du peuplier hybride relativement aux conditions de compétition et de distribution spatiale des ressources. Les conclusions de chaque chapitre sont détaillées ci-après et se trouvent résumées dans le Tableau 5.1. Par la suite, des retours sur les objectifs généraux de recherche et sur l'état des connaissances seront présentés. Les implications pratiques de la recherche ainsi que ses implications novatrices seront finalement soulignées, avant de proposer de nouvelles pistes de recherche qui mériteraient d'être explorées.

La recherche a été menée, dans un premier temps (chapitres I et II), sur huit sites de plantations expérimentales dans la région du Saguenay – Lac-Saint-Jean, couvrant une superficie totale de 40 hectares. Les résultats obtenus au chapitre I concernant l'effet des techniques sylvicoles sur le peuplier hybride ont été approfondis et expliqués par la méthodologie utilisée dans le chapitre II, c'est-à-dire les excavations de racines et les analyses de la dynamique de l'azote dans le sol à différentes profondeurs. Dans un deuxième temps (chapitre III), les processus de prolifération racinaire et de réponse à la compétition et à la fertilité du sol qui avaient été observés sur le terrain ont été validés et explorés plus en détail lors d'une expérience en pots.

5.1 Conclusions par chapitre

Le chapitre I a démontré qu'il y a des disparités entre les différentes techniques d'aménagement sylvicole de plantations. En effet, elles n'ont pas toutes la même

efficacité à créer des conditions de croissance optimales pour le peuplier hybride. Parmi les trois techniques d'aménagement testées, soit la préparation mécanique du sol, le contrôle de la compétition végétale et la fertilisation, c'est la première qui a démontré le plus d'avantages. De plus, de toutes les méthodes de préparation mécanique du sol, c'est celle des monticules qui s'est avérée être la meilleure pour assurer la survie et la croissance des peupliers. Cet avantage s'expliquait notamment par un sol plus chaud et plus meuble, une minéralisation accrue de l'azote, et une réduction importante de la végétation compétitrice dans les monticules. Tous ces facteurs ont probablement favorisé un développement accru du système racinaire – ce qui sera effectivement démontré dans le chapitre suivant.

Sur la base de ces résultats, nous proposons que, dans le cadre de l'aménagement de plantations d'arbres à croissance rapide, la priorité d'utilisation des techniques sylvicoles soit établie ainsi : préparation mécanique du sol (PMS) > contrôle de la compétition végétale aérienne (CC) > fertilisation. Nous suggérons cette séquence parce que la PMS s'est avérée être le meilleur moyen de créer des microsites de sol favorables à la plantation, de réduire grandement la végétation compétitrice présente préalablement sur le site, et de contribuer fortement à l'établissement, la survie, et la croissance des arbres. L'écart entre la meilleure méthode de PMS et l'absence de PMS était du simple au double pour ce qui est de la croissance en hauteur des peupliers. Le contrôle de la compétition et la fertilisation, tels qu'appliqués dans cette étude, ont eu des effets appréciables (i.e., gains de 25 % pour la croissance en hauteur), mais n'ont pas pu compenser une PMS inadéquate. Lorsque ces deux traitements étaient utilisés conjointement sur des sites non préparés, les arbres n'atteignaient que la moitié de la hauteur de ceux qui étaient plantés sur monticules, mais ne recevant ni CC ni fertilisation.

Les résultats du chapitre I et les suggestions pour l'aménagement qui en découlent concordent avec les quelques autres études ayant comparé une étendue semblable de techniques d'aménagement en interaction, mais avec d'autres espèces d'arbres et dans des environnements différents (Carter et Foster, 2006 ; Nilsson et Allen, 2003 ; Zhao *et al.*, 2009). Parmi ces techniques, la PMS par création de monticules semble offrir les meilleurs rendements lors de la période juvénile grâce à un développement rapide des racines, un fort

taux de survie des plants, une réduction importante de la végétation compétitrice, une minéralisation substantielle d'azote, et aucune mortalité. De plus, ses effets étaient toujours observables après quelques années et semblaient vouloir persister au-delà de la période étudiée. La grande intolérance du peuplier hybride à la compétition souterraine pourrait expliquer pourquoi la PMS est si primordiale pour cette espèce. Dans les conditions où le contrôle de la compétition serait considéré comme nécessaire, il pourrait être limité à la deuxième année après la plantation afin de réduire les coûts de débroussaillage et maximiser la croissance. La fertilisation ne devrait être envisagée que si une PMS intensive est également effectuée, car si la PMS n'est pas intensive, la fertilisation n'a pas d'effet car le système racinaire des arbres n'est pas suffisamment développé pour capter l'entièreté de cet apport en éléments nutritifs, ou du moins le capter avant les autres plantes et les microorganismes du sol, ou avant qu'il ne soit immobilisé dans la matière organique du sol.

Le chapitre II a permis d'observer les conditions micro-environnementales du sol et les relations entre celles-ci et le développement des racines, pour expliquer l'effet bénéfique des monticules observé au chapitre I. Pour ce faire, la technique par monticules a été comparée à l'autre extrémité du gradient de préparation mécanique du sol, c'est-à-dire les sols non préparés.

Les monticules ont procuré plusieurs avantages nutritifs et environnementaux en comparaison avec les sols non préparés. Premièrement, en enfouissant l'horizon organique de surface sous une quantité de sol minéral, le processus de création du monticule a fortement réduit la végétation compétitrice et libéré l'espace dans cet horizon riche en éléments nutritifs. Les racines du peuplier hybride ont alors pu explorer cet espace et en acquérir les ressources en nutriments. Par contre, dans les sols non préparés, les racines de peupliers ont évité l'horizon organique – naturellement situé à la surface. Bien que l'horizon organique des sols non préparés contienne une quantité plus élevée d'éléments nutritifs que celui du monticule, il est aussi abondamment colonisé par des racines d'autres espèces. Cette divergence dans le comportement des racines est révélatrice de l'évitement de la compétition par le peuplier hybride. Il s'agit là d'une caractéristique incontournable de l'espèce, qui devrait toujours être considérée lors des plantations.

Deuxièmement, la couche minérale de surface du monticule a démontré un taux relativement élevé de minéralisation de l'azote, et ce, malgré une quantité de matière organique et un contenu total en azote inférieurs à ceux de l'horizon organique de surface d'un sol non préparé. Ainsi, même si le contenu en azote total et la matière organique sont diminués dans le monticule, la minéralisation de l'azote, elle, augmente. L'azote minéralisé, donc sous forme inorganique, est assimilable par la plante, mais sa présence en forêt boréale est limitée. La technique par monticules vient pallier ce manque en azote, ce qui constitue un avantage certain pour la plante.

Troisièmement, les conditions de sol meubles et chaudes qui sont typiques des monticules ont favorisé la production de racines et leur élongation, ce qui a par la suite permis aux peupliers hybrides d'avoir accès à un plus large volume de sol et un plus grand réservoir de nutriments.

Quatrièmement, cette allocation supérieure de biomasse aux racines chez les arbres plantés sur monticules a été immédiatement récompensée par une acquisition supérieure d'azote. Cela a dû augmenter les taux de photosynthèse et la croissance générale des arbres, expliquant l'efficacité particulière de cette technique de préparation mécanique du sol.

Puisque les chapitres I et II tendent à démontrer l'importance de la distribution spatiale des nutriments dans le sol et celle de l'évitement de la compétition, le comportement des racines du peuplier hybride a été examiné plus en détail dans l'expérience en pots rapportée au chapitre III. Cette expérience en pots a établi la manière dont interagissent ces deux facteurs primordiaux sur les racines du peuplier hybride, alors mis en compétition (ou non) avec la graminée *Calamagrostis canadensis*. L'expérience incluait également des sols avec une distribution homogène ou hétérogène des nutriments.

Les peupliers hybrides ont effectivement réagi à la présence de compétition et à la distribution spatiale des nutriments. La compétition avait un impact globalement négatif sur le développement de la tige et des racines. Le comportement d'évitement de la compétition racinaire a donc été confirmé pour le peuplier hybride.

Toutefois, ce comportement était moins prononcé quand la moitié du pot occupée par la graminée renfermait autant ou davantage de nutriments que la moitié du pot où se trouvait le peuplier. Parmi les traitements de distribution spatiale de nutriments, c'est donc le traitement homogène qui a eu l'effet le plus bénéfique sur le développement de la tige et des racines des peupliers. Cette homogénéité a présenté le meilleur compromis avec, d'une part, une quantité de nutriments dans la zone de sol initiale suffisamment grande pour appuyer le développement des racines vers les zones de sol éloignées, et d'autre part, une quantité de nutriments dans les zones éloignées suffisamment attirante pour rentabiliser le déploiement de racines exploratrices. À l'opposé, la distribution hétérogène où les nutriments étaient concentrés au pied du peuplier a été la moins avantageuse, car l'expansion du système racinaire s'est limitée principalement à cette zone initiale, donnant ainsi accès à un volume de sol inférieur et donc une quantité possiblement moindre de nutriments. L'avantage de la distribution homogène pour le système racinaire a même permis, en présence de compétition, une croissance de la tige équivalente à celle des traitements sans compétition.

Les racines exploratrices déployées dans les zones les plus riches en nutriments se distinguaient par une architecture particulière, pour laquelle la fréquence de production de liens racinaires externes le long d'une branche principale était supérieure, tout comme la proportion de liens externes sur le nombre total de liens racinaires. Les liens externes sont ceux qui se terminent par un méristème (i.e., une pointe), et sont considérés comme étant les plus actifs au niveau de l'absorption des nutriments. Par conséquent, une architecture racinaire qui privilégie ces liens témoigne d'une grande plasticité du peuplier hybride en réponse à la présence de compétition et à la distribution spatiale des nutriments du sol.

La distribution spatiale des nutriments a influencé l'étendue de l'exploration du sol par les racines, puisque les arbres dont l'environnement de sol initial était plus riche que le reste du pot présentaient une prolifération des racines et une exploration du sol plus limitées. Ceci se manifestait par une architecture racinaire représentative de conditions défavorables. Au contraire, les arbres plantés dans des conditions initiales équivalentes ou plus pauvres que les zones de sol éloignées avaient tendance à explorer davantage les zones de sol éloignées et à

développer une architecture racinaire typique d'une absorption supérieure, comme celle décrite dans le paragraphe précédent.

De manière générale, les peupliers hybrides se sont mieux développés lorsque les deux conditions suivantes étaient réunies : 1) une source de nutriments au sein de leur zone de sol de départ qui est suffisante pour appuyer le développement initial de l'arbre (i.e., ne pas se trouver dans la moitié du pot la plus pauvre) et 2) une source de nutriments dans les zones de sol éloignées qui est suffisante pour attirer les racines exploratrices et rentabiliser l'expansion du système racinaire (i.e., que la moitié opposée du pot ne soit pas la plus pauvre). Par conséquent, une distribution spatiale homogène des nutriments s'est avérée dans le cas étudié un compromis valable par rapport aux deux conditions ci-dessus. La distribution homogène a permis au peuplier hybride de bénéficier d'un large volume de sol grâce à une exploration extensive par les racines, ce qui a probablement garanti par la suite un accès à un réservoir total de nutriments plus grand, dont le résultat a été une croissance aérienne supérieure.

Par-dessus tout, la distribution spatiale des nutriments a interagi avec le niveau de compétition au point de modifier le dénouement de la compétition. Cette interaction est dévoilée par la similarité au niveau du développement de la tige et des racines entre 1) les arbres croissant en absence de compétition et avec une distribution spatiale hétérogène des nutriments où ceux-ci sont concentrés dans l'environnement immédiat de l'arbre, et 2) les arbres croissant en présence de compétition et avec une distribution spatiale homogène des nutriments.

Le tableau 5.1 à la fin de cette section résume les conclusions de chacun des chapitres, telles que présentées ici.

5.2 Retour sur les objectifs généraux

Les objectifs généraux de cette étude, présentés dans la section 1.2 et repris brièvement ici, ont été atteints. Ils seront décortiqués ici un par un. Ces conclusions globales s'avèrent l'amalgame des différents chapitres de cette thèse.

Objectif 1 : déterminer les conditions environnementales favorables au peuplier hybride

Les conditions environnementales qui optimisent l'établissement, la survie, et la croissance juvénile du peuplier hybride sont celles qui favorisent le développement des racines de peuplier. Ces conditions sont : *i*) un sol meuble et chaud; *ii*) une végétation compétitrice peu abondante; *iii*) des taux élevés de minéralisation de l'azote du sol; *iv*) un réservoir de nutriments disponibles qui est atteignable par les racines du peuplier et libre de compétiteurs; et *v*) une distribution spatiale des nutriments assez large, plutôt que concentrée dans l'environnement immédiat de l'arbre, de manière à obliger les racines de ce dernier à s'allonger pour atteindre les nutriments. En effet, le développement de la tige du peuplier hybride bénéficie ultimement d'un système racinaire étendu donnant accès à un large volume de sol. Même si la concentration de nutriments dans le sol est faible, si les racines explorent un large volume de sol, elles trouveront une quantité de nutriments assez grande. Un système racinaire étendu permet aussi de profiter au maximum d'un apport en fertilisants, de maintenir une bonne croissance lorsque l'effet de la fertilisation ne se fera plus sentir après un ou deux ans, et potentiellement, de mieux résister à un stress environnemental, comme une sécheresse.

Objectif 2 : identifier les techniques d'aménagement sylvicole permettant d'atteindre les conditions favorables au peuplier hybride

Les meilleures techniques d'aménagement sylvicole des plantations sont celles qui créent les conditions environnementales énumérées ci-dessus. Les différentes techniques d'aménagement étudiées ont interagi entre elles, avec des impacts variables selon les conditions induites par les traitements. Par exemple, le contrôle de la compétition végétale a été proportionnellement moins efficace lorsqu'il est jumelé à des préparations mécaniques du sol plus intensives, car celles-ci éliminent déjà une grande partie de la végétation compétitrice.

Au final, il paraît même légitime de remettre en question la pertinence d'utiliser certaines des techniques d'aménagement sylvicole. Ces résultats de recherche auront d'importantes

implications pour les futures stratégies d'aménagement des plantations de peupliers hybrides en région boréale. Cependant, d'autres considérations, comme les coûts, les conditions de travail de la main-d'œuvre, etc., seront aussi importantes dans le processus décisionnel qui entoure l'aménagement des plantations.

Objectif 3 : interpréter la réaction du peuplier hybride aux conditions induites par l'aménagement

De manière générale, le peuplier hybride répond à la compétition racinaire par une stratégie d'évitement très prononcée. Toutefois, il démontre aussi une certaine plasticité racinaire en réponse à la distribution spatiale des nutriments du sol. Ces deux réponses peuvent se combiner pour donner des résultats parfois surprenants. Par exemple, lorsque la zone de sol occupée par la compétition contient une quantité de nutriments disponibles assez grande pour rentabiliser la production de racines exploratrices, le comportement d'évitement est alors moins prononcé, même s'il est toujours présent.

5.3 Retour sur l'état des connaissances

Dans l'introduction, plusieurs théories ont été avancées pour établir le cadre de la recherche. Il s'impose maintenant de faire un retour sur ces connaissances théoriques, en les comparant avec les résultats obtenus par cette recherche. La conclusion théorique est organisée en général selon les chapitres et porte plus particulièrement sur les racines.

Tout d'abord, cette thèse n'avait pas pour but de départager les théories de Grime et Tilman sur la compétition végétale, mais elle avait la prétention d'utiliser les deux, en parallèle, selon les situations. Grime s'attardait davantage à l'importance de la compétition, tandis que Tilman, lui, insistait sur son intensité. Dans cette étude, quand l'attention était portée sur la compétition, que ce soit sur le terrain ou en pots, c'est la théorie de Tilman qui s'appliquait à la recherche. La différence entre la réponse à la présence de compétition pour le peuplier et l'absence de compétition correspond à l'intensité. Par contre, lorsque c'est la réponse à la compétition du peuplier en comparaison avec la distribution spatiale des nutriments, c'est

plutôt l'importance de la compétition végétale – donc la théorie de Grime –, qui soutenait la recherche. En somme, les théories de Grime et Tilman sur la compétition végétale ne sont pas incompatibles et demeurent toujours pertinentes pour une recherche comme celle menée ici.

Par ailleurs, cette étude a confirmé que les racines de peupliers hybrides manifestent un comportement d'évitement de la compétition pour les ressources du sol. Ce comportement du peuplier hybride rejoint les théories de l'évitement (Messier *et al.*, 2009a) et de la ségrégation racinaire (Schenk *et al.*, 1999), mais s'oppose à la théorie de l'agrégation des racines (Bartelheimer *et al.*, 2006). Par contre, d'autres espèces pionnières ou à croissance rapide pourraient potentiellement exhiber un comportement semblable.

Cette étude a aussi contribué à une meilleure compréhension de la prolifération optimale des racines (Hodge *et al.*, 1999) par rapport à divers patrons de distribution spatiale des ressources du sol, particulièrement en présence de compétition. La prolifération racinaire chez le peuplier hybride s'est exprimée par la modification de certaines caractéristiques de l'architecture des racines. Puisque ces caractéristiques sont indépendantes de la taille du système racinaire (Berntson, 1994), elles suggèrent que l'adaptation plastique du peuplier hybride à son environnement se manifeste au niveau de son architecture racinaire, et ceci de manière assez subtile. Cet exemple en rejoint d'autres (Kembel et Cahill, 2005 ; Rajaniemi et Reynolds, 2004) ayant rapporté des observations divergentes de l'idée initiale de Grime (Grime *et al.*, 1986), qui proposait que les espèces présentant de forts taux de croissance comptaient plutôt sur des adaptations morphologiques. Par ailleurs, Fitter et al. (1991) ont affirmé que l'élongation des liens racinaires internes et externes est synonyme d'une exploitation plus efficace du sol. Pourtant, dans le cas présent, une production plus fréquente de liens racinaires externes a possiblement été pour les peupliers hybrides la manière la moins coûteuse d'acquérir les nutriments situés dans la zone de sol occupée par le compétiteur.

En concordance partielle avec Berntson (1994), dans la présente étude, la taille du système racinaire des peupliers a exprimé la réaction à la compétition, mais ce sont les caractéristiques architecturales indépendantes de la taille du système qui ont été les plus

révélatrices de l'adaptation à la distribution spatiale des nutriments. Toujours selon Berntson (1994), la direction du déploiement des racines, quant à elle, pourrait démontrer le compromis atteint lors du choix entre prioriser la réaction à la compétition ou celle aux ressources. L'absence de compétition pourrait avoir permis au peuplier d'optimiser l'étendue de l'exploitation des ressources du sol, tandis que la présence de compétition aurait possiblement forcé le peuplier à démontrer davantage d'efficacité.

L'interaction entre la compétition végétale et la distribution spatiale des ressources pourrait aussi être comparée à ce que Cahill et al. (2010) ont appelé « l'intégration des informations » concernant l'environnement de la plante, ainsi que la « hiérarchie de prise de décisions » en réaction aux informations. Dans cette étude, les résultats suggèrent que la compétition revêt davantage d'importance que la fertilité du sol, car plusieurs des caractéristiques des racines présentent l'écart le plus grand entre les traitements de présence et d'absence de compétition, alors que les traitements de distribution spatiale de nutriments entraînent des variations moindres. Par conséquent, le peuplier hybride dans son patron de décision commence par considérer s'il y a de la compétition. La distribution spatiale des nutriments devient une considération secondaire. De tels mécanismes signifient que les plantes doivent posséder une quelconque habileté pour sonder, analyser, et le cas échéant, ajuster la réponse à l'environnement. Cette manière de faire des plantes pourrait être comparée à celle des animaux en quête de nourriture qui adaptent leurs stratégies de recherche en fonction de nouvelles informations acquises.

5.4 Implications pratiques pour la foresterie

Les réponses des peupliers hybrides qui ont été rapportées dans cette thèse seront importantes à considérer pour l'aménagement du sol de futures plantations sous sylviculture intensive. Le sol et les racines semblent être les aspects les plus importants en vue d'assurer un développement satisfaisant du peuplier hybride. Un aménagement visant à induire un réarrangement vertical des horizons de sol pourrait améliorer l'accès aux ressources du sol et optimiser la croissance aérienne des arbres pionniers à croissance rapide. Un tel aménagement du sol pourrait aussi s'avérer être une alternative à certaines méthodes de

contrôle de la compétition qui nécessitent plus d'investissements en efforts et en temps, et qui sont potentiellement plus dommageables pour l'environnement, comme de fortes doses d'herbicides ou des méthodes mécaniques intensives qui enlèvent les horizons organiques de surface.

Le tableau 5.2 compare les résultats de cette recherche doctorale avec d'autres études nord-américaines concernant des peupliers hybrides en zone tempérée ou boréale, et sur sites agricoles ou forestiers. Le tableau présente le détail des techniques d'aménagement spécifiques à chacune des études et les rendements en croissance des arbres. Les croissances en hauteur annuelles moyennes servent de repères pour bien comparer ces études entre elles. Le tableau montre que les peupliers plantés sur des monticules (Bilodeau-Gauthier *et al.*, 2011) se classent parmi les meilleurs sur les sols forestiers, et arrivent dans la moyenne en comparaison des plantations en sol agricole. Cependant, le tableau montre également que les peupliers plantés sur des sols non préparés obtiennent les pires rendements.

Ainsi, les résultats de cette recherche sont encourageants, puisqu'ils démontrent que le peuplier hybride est capable de performer relativement bien sur des sols forestiers boréaux lorsque les conditions favorables sont réunies grâce à un aménagement adéquat, et particulièrement grâce à la technique de préparation du sol par monticules.

5.5 Caractère novateur de la recherche et pistes à explorer

Cette recherche est parmi les premières à démontrer l'interaction entre la compétition et la distribution spatiale des nutriments chez une espèce d'arbre. En effet, cette recherche établit que, dans le cas du peuplier hybride, autant en milieu naturel que contrôlé, les réponses à la compétition et à la distribution spatiale des nutriments, prises individuellement, sont différentes de la réponse à la combinaison des deux facteurs. Le développement des plantes est ainsi influencé par leurs réponses à ces deux facteurs combinés. La manière dont se comportent les plantes en présence de compétition est donc très dépendante des conditions environnementales dans lesquelles elles se trouvent. La répartition des ressources dans l'environnement force la plante à utiliser certaines stratégies d'occupation du territoire, qui

ont un impact sur ses interactions avec les autres individus. Les deux facteurs sont intrinsèquement liés, et ne devraient pas être considérés l'un sans l'autre. Les considérer séparément pourrait mener à une interprétation et une compréhension erronées des phénomènes écologiques. Le peuplier hybride est probablement représentatif de la réponse des autres espèces pionnières ou à croissance rapide. Toute espèce sensible à la compétition et ayant des besoins nutritifs élevés pourrait démontrer le même comportement que celui du peuplier hybride, et réagir de la même manière à la répartition spatiale des ressources et à la présence de compétition. Il n'est donc pas simplement question ici d'un comportement propre à une espèce, mais plutôt d'une relation entre un arbre, le sol et ses voisins.

Cette étude permet également de proposer une façon novatrice de voir l'aménagement des plantations d'arbres, au Québec et ailleurs dans le monde. Dorénavant, l'aménagement sylvicole, notamment les plantations à croissance rapide, devrait être planifié en tenant compte, non seulement de l'écologie des espèces, mais aussi des stratégies de réponses et d'adaptation de celles-ci à leur environnement. Les résultats de cette étude démontrent qu'il est possible d'aménager l'environnement de manière à susciter une réponse plastique chez les arbres. Cette plasticité leur permettrait de tirer profit de façon optimale des ressources disponibles. Même dans un environnement de prime abord peu favorable, un aménagement du sol adéquat, visant à induire une répartition spatiale particulière des ressources, pourrait forcer l'espèce plantée à croître davantage. Ce faisant, elle accèderait à un réservoir supérieur de ressources. Ceci serait une manière d'améliorer les conditions environnementales sans pour autant s'en remettre à des apports en fertilisants. Néanmoins, la possibilité pour l'arbre de profiter pleinement d'un tel aménagement serait aussi reliée à la présence de végétation compétitrice. Il apparaît néanmoins réaliste de réduire la compétition sans recourir aux herbicides, et même de combiner cette action à celle de l'amélioration des conditions de fertilité. Une planification qui tiendrait compte de ces nouvelles données scientifiques permettrait d'assurer le succès des plantations à croissance rapide, une condition gagnante du zonage forestier. Cette conception de la foresterie favorisera la pérennité de la ressource forestière et le développement socioéconomique des régions qui en dépendent.

Par ailleurs, cette recherche invite à concevoir les plantes comme étant capables d'analyser l'information provenant de leur environnement. Ce faisant, elle abonde dans le sens de la récente étude de Cahill et al. (2010). Il s'agit d'une idée nouvelle qui circule depuis peu dans le milieu de la recherche sur les végétaux et qui mériterait qu'on s'y attarde davantage. En effet, cela signifie que la plante n'est pas passive par rapport à son environnement, et donc, que sa capacité d'adaptation pourrait être beaucoup plus grande qu'elle n'a été imaginée jusqu'à maintenant. Cette piste mérite d'être explorée – et mieux comprise – dans les années à venir. Par exemple, pour véritablement conclure que les plantes sont capables de « comportements », i.e., d'une capacité d'analyse et de réponse à leur environnement, il faudrait concevoir un dispositif expérimental qui permettrait de détecter un changement dans le développement, la morphologie ou l'architecture d'un *même individu* lorsqu'il entre en contact avec des conditions environnementales qui varient dans le temps ou l'espace. Par opposition, des changements entre différents individus soumis à différentes conditions pourraient n'indiquer que la plasticité de l'espèce, et non un comportement en tant que tel.

Également, il apparaît important de souligner d'autres pistes de recherche à envisager, découlant du travail présenté ici. La première piste proposée porterait sur les stimuli et mécanismes d'adaptation des racines aux conditions environnementales du sol. Par exemple, une question à explorer serait : les racines d'espèces à croissance rapide pourraient-elles démontrer des adaptations physiologiques aux conditions environnementales en modifiant leur capacité d'absorption des nutriments? La seconde piste proposée se pencherait davantage sur la répartition spatiale idéale des ressources pour chaque espèce. Ces recherches viseraient par exemple à répondre à la question suivante : existe-t-il une seule répartition idéale, ou bien chaque espèce et chaque environnement requièrent-ils une répartition unique?

Tableau 5.1 Résumé des objectifs, thèmes abordés et conclusions atteintes pour chaque chapitre.

Chapitre	Objectif	Thèmes abordés	Conclusions
I	Évaluer sur le terrain la réponse du peuplier hybride (PEH) aux techniques d'aménagement sylvicoles (préparation mécanique du sol (PMS), contrôle de la compétition végétale, et fertilisation, ainsi que leurs interactions).	1) Un aménagement sylvicole adéquat permet de créer des microsites favorables à l'établissement, la survie et la croissance des arbres.	La préparation par monticules s'est avérée être la meilleure technique d'aménagement sylvicole pour assurer la survie et la croissance des peupliers, puisqu'elle offre les meilleurs gains en croissance. De manière générale, il est recommandé de favoriser les opérations dans l'ordre : préparation mécanique du sol > contrôle de la compétition > fertilisation.
II	Évaluer sur le terrain le développement racinaire du PEH en réponse à la distribution spatiale des horizons de sol induit par la PMS, la dynamique de l'azote, et la présence de racines compétitives.	1) Évitement de la compétition; 2) Prolifération des racines dans les zones de sol fertiles; 3) Amélioration de la minéralisation de l'azote par la PMS.	1) Les racines du PEH démontrent un comportement d'évitement de la compétition pour les ressources. 2) Les racines prolifèrent préférablement (et dans cet ordre) dans les zones de sol *i*) dénuées de compétition et *ii*) riches en azote disponible et avec des taux de minéralisation élevés. 3) Malgré des concentrations totales et une disponibilité inférieures en azote, les monticules présentent des taux de minéralisation et un réservoir total d'azote disponible supérieurs par rapport aux sols non préparés (et non perturbés) contenant davantage de matière organique. 4) L'avantage du monticule est de permettre un meilleur développement initial du système racinaire, de fournir un large volume de sol dénué de compétition et qui représente un grand réservoir de nutriments disponibles. Le tout permet de maximiser la croissance de la tige du peuplier hybride.

III	Évaluer lors d'une expérience en pots la réponse des racines du PEH à la compétition et à la distribution spatiale des nutriments du sol.	1) Évitement de la compétition; 2) Prolifération des racines dans les zones de sol fertiles; 3) Compromis entre les deux précédents comportements; 4) Avantage d'une distribution hétérogène des nutriments pour la croissance totale de l'arbre.	1) Les racines du PEH démontrent un comportement d'évitement de la compétition pour les ressources. 2) et 3) Les racines prolifèrent préférablement (et dans cet ordre) dans les zones de sol *i*) dénuées de compétition et *ii*) riches en azote disponible et avec des taux de minéralisation élevés. 4) La distribution homogène s'est avérée le meilleur compromis avec, d'une part, une quantité de nutriments dans la zone de sol initiale suffisamment consistante pour appuyer le développement des racines, et d'autre part, une quantité de nutriments dans les zones plus éloignées suffisamment attirante pour rentabiliser le déploiement de racines exploratrices. À l'opposé, la distribution hétérogène où les nutriments étaient concentrés au pied du peuplier a été la moins avantageuse, en limitant l'expansion du système racinaire, donnant accès à volume de sol inférieur, possiblement une quantité moindre de nutriments, et résultant finalement en une croissance inférieure de la tige.

Tableau 5.2 Comparaison de la croissance de peupliers hybrides dans plusieurs études réalisées au Québec et au Canada.

Référence	Habitat	Préparation mécanique du sol	Contrôle de la compétition	Fertilisation	Type de plant †	Hauteur totale (m)	Hauteur initiale (m)	Croissance en hauteur annuelle moyenne (m)
Québec								
La présente étude (monticule)	forestier	monticule	débroussaillage		PRN	4.5 m à 5 ans	1	0.7
La présente étude (non préparé)	forestier	aucune	débroussaillage		PRN	2.5 m à 5 ans	1	0.3
Bona et al., 2008	forestier	scarifiage	Aucun	oui	PRN	nd ‡	1 à 2	nd
Coll et al., 2007	forestier	herse	débroussaillage, herbicide, rotoculteur		PRN	2.5 m à 2 ans	1.2	0.65
Côté et Camiré, 1984, 1985, 1987	agricole	labour +herse	Rotoculteur		B	2.5 m à 3 ans	0.1	0.8
DesRochers et Tremblay, 2009	agricole	labour +scarifiage	scarifiage, rotoculteur	oui	PRN	1.8 m à 2 ans	1.15	0.65
Fortier et al., 2010a, 2010 b	agricole	aucune	herbicide à la plantation		PRN	14 m à 6 ans	1.65	2.1
Guillemette et DesRochers, 2008	forestier et agricole	labour +scarifiage	Aucun	oui	PRN	2 m à 2 ans	1.2	0.4

Rivest et al., 2009	agricole	aucune	paillis de polyéthylène	oui	B	12.7 m à 7 ans	0.05	1.8
Sigouin 2008	forestier et agricole	labour +scarifiage, suivi de monticule ou herse	Rotoculteur	oui	PRN	2 m à 3 ans	0.5	0.5
Canada								
Amichev et al 2010	agricole	scarifiage	débroussaillage, herbicide, rotoculteur		BR	12.5 m à 11 ans	0.05	1.13
Block et al., 2009	agricole	scarifiage +rotoculteur	Herbicide	oui	BR	2 m à 3 ans	0.05	0.65
Brown et al., 1996	agricole	labour	Rotoculteur	oui	B	1.4 m à 1 yr	0.05	1.35
Brown et van den Driessche, 2005	forestier	aucune	Scarifiage	oui	B	7 m à 4 ans	0.05	1.75
Pinno et Bélanger, 2009	agricole	aucune	débroussaillage, herbicide, rotoculteur		PRN	2 m à un an	1	1
Pinno et al., 2009	agricole	aucune	herbicide +scarifiage		PRN	3-4 m à 4 ans	1	0.85

van den Driessche, 1999	forestier	aucune	Scarifiage	oui	B	1.8 m à 1 yr	0.15	1.65
van den Driessche et al., 2005	agricole	labour +monticule	Rotoculteur	oui	B	3 m à 4 ans	0.05	0.75
van den Driessche et al., 2008	agricole	labour +rotoculteur	Rotoculteur	oui	BR	7 m à 6 ans	0.05	1.17

† B : bouture; BR : bouture avec racines; PRN : plançon à racines nues.

‡ nd : non disponible.

APPENDICE A

DONNÉES SUPPLÉMENTAIRES NON PRÉSENTÉES DANS LES CHAPITRES PRINCIPAUX

Table A.1 Data on the natural stands that were present on the study sites prior to the establishment of the hybrid poplar plantations.

Block *	Stand code †	Dominant species ‡	Density §	Height of dominant trees	Stand age
			%	m	yrs
1 LT1	Pe A3 50	aspen	80-100	12-17	50
2 LT2	Fi B3 30	aspen, birch	60-80	12-17	30
3 PR1	PeE A2 70	aspen, black spruce	80-100	17-22	70
4 PR2	PeE A2 70	aspen, black spruce	80-100	17-22	70
	Pe B2 70	aspen	60-80	17-22	70
5 OU1	Pe C2 70	aspen	40-60	17-22	70
6 OU2	PeE B2 70	aspen, black spruce	60-80	17-22	70
7 BS1	PeBb B3 50	aspen, birch	60-80	12-17	50
8 BS2	PeBb B2 50	aspen, birch	60-80	17-22	50

* The eight blocks that are the topic of chapters I and II. Block No 4 was covered by two different stand types.

† The code used to identify the sites on the ecoforestry maps produced by the Ministère des Ressources naturelles et de la faune du Québec.

‡ Dominant species constitute at least 50% of the stand area.

§ The density of the canopy, where 100% represents a completely closed canopy.

Table A.2 Characteristics of the competition cover as affected by mechanical soil preparation (MSP) in the year after planting (2005), assessed in a 1-m radius around hybrid poplars. Competition cover was computed as a percentage of the sampled surface area, and was classified by the type of plant species encountered: herbaceous = herbaceous, non-woody species; woody/tree = woody species that may grow as tall as trees; woody/bush = woody species that do not grow as tall as trees; grasses = graminoid species (e.g., Poacea, Carex); debris = non-living debris, e.g., harvest residue, woody debris, rocks; bare soil = non-vegetated. See Chapter I for details of the methods.

Variable		Soil Preparation				
		Unprepared	Light disk trenching	Heavy disk trenching	Harrow	Mounding
Maximum height of competitors	m	4.26	2.39	2.13	1.97	2.37
	SD	2.0	1.3	1.0	1.3	2.0
No of shoots of woody/ tree competitors	–	12.5	28.7	36.4	30.7	44.4
	SD	9.5	16.9	12.9	20.5	8.9
Competition cover						
Woody/tree	%	2.75	5.38	2.83	16.2	3.44
	SD	5.1	5.3	3.1	17.6	4.0
Woody/bush	%	1.04	0.83	0.74	0.77	0.81
	SD	0.18	0.22	0.12	0.22	0.23
Herbaceous	%	25.4	14.6	12.7	8.92	12.7
	SD	10.6	8.6	5.8	6.2	10.8
Grasses	%	3.11	2.32	1.88	1.41	0.99
	SD	4.9	2.8	2.3	1.5	1.4
Debris	%	37.1	35.0	29.1	34.0	29.2
	SD	14.0	13.0	8.7	13.0	10.3
Bare soil	%	18.9	13.8	17.0	8.78	9.37
	SD	11.8	5.4	8.6	6.2	5.1

Table A.3 Chemical analyses of hybrid poplar leaves for the years 3 and 4 (2006 and 2007). Values are means from 8 sites; SD = standard deviation. In year 3, one leaf per tree and for the 12 trees in a subplot formed a pooled sample per subplot. Leaf sampling in year 4 is explained in chapter I. For both years, analytical methods were the same as those described in chapter I. Empty cells indicate that the analysis was not done for that sample.

Year	Season	Treatments		Foliar C		Foliar N		Foliar P		Foliar K		Foliar Ca		Foliar Mg	
		Soil Preparation	Vegetation Control	%	SD	%	SD	g kg^{-1}	SD	g kg^{-1}	SD	g kg^{-1}	SD	g kg^{-1}	SD
Year 3 (2006)	Summer	Unprepared													
			all	45.65	9.2	1.31	0.2	1.39	0.5	8.40	2.5	6.68	2.3	1.45	0.5
			never	47.32	3.4	1.22	0.2	1.35	0.3	8.97	1.5	6.35	1.7	1.24	0.4
			year 3	47.14	2.9	1.26	0.2	1.28	0.7	7.19	3.4	6.31	3.1	1.38	0.7
			year 2+4	47.17	3.5	1.36	0.1	1.68	0.6	8.75	2.5	7.35	2.8	1.60	0.7
			years 2+3+4	40.55	18.2	1.39	0.2	1.22	0.3	8.79	2.2	6.66	1.2	1.57	0.4
		Light disk trenching													
			all	47.40	2.9	1.31	0.1	1.49	0.3	10.72	3.3	6.62	3.0	1.82	0.7
			never	47.42	3.4	1.25	0.1	1.53	0.3	9.92	4.0	8.10	3.8	2.25	1.2
			year 3	47.33	3.1	1.27	0.2	1.47	0.4	10.51	3.2	6.54	3.6	1.62	0.6
			year 2+4	47.33	3.0	1.37	0.1	1.58	0.4	12.11	4.1	5.80	1.9	1.72	0.2
			years 2+3+4	47.51	3.0	1.36	0.1	1.40	0.2	10.33	1.6	6.03	2.3	1.70	0.3
		Heavy disk trenching													
			all	47.81	1.8	1.39	0.1	1.56	0.3	12.32	2.6	5.87	1.8	1.57	0.3
			never	47.71	1.4	1.37	0.1	1.72	0.3	13.68	2.6	6.41	1.7	1.66	0.4
			year 3	47.23	3.0	1.33	0.1	1.49	0.2	11.58	2.5	5.05	1.6	1.44	0.3
			year 2+4	48.04	1.4	1.43	0.2	1.59	0.2	12.11	2.5	6.27	2.1	1.68	0.4
			years 2+3+4	48.25	1.0	1.44	0.1	1.43	0.3	11.93	2.9	5.75	1.9	1.52	0.2
		Harrow													
			all	47.24	3.0	1.35	0.1	1.52	0.4	9.99	3.3	7.53	2.7	2.11	0.6
			never	47.25	3.4	1.30	0.1	1.39	0.2	8.24	1.9	7.26	2.2	2.07	0.7

			year 3	47.41	3.1	1.34	0.1	1.67	0.3	10.21	4.0	7.55	2.0	2.08	0.8
			year 2+4	47.30	3.0	1.41	0.2	1.43	0.7	10.19	3.3	7.96	3.9	2.20	0.7
			years 2+3+4	46.99	3.3	1.37	0.1	1.59	0.2	11.09	3.4	7.31	2.7	2.10	0.4
		Mounding													
			all	48.02	0.8	1.52	0.1	1.57	0.4	11.81	3.7	7.21	3.1	1.89	0.4
			never	47.84	0.8	1.47	0.1	1.49	0.5	11.02	2.9	7.59	3.9	1.80	0.3
			year 3	47.97	0.8	1.45	0.1	1.58	0.4	11.25	3.5	7.46	2.1	1.97	0.4
			year 2+4	48.09	0.9	1.55	0.1	1.54	0.5	11.75	4.1	7.38	3.8	1.82	0.3
			years 2+3+4	48.16	0.8	1.60	0.1	1.68	0.5	13.20	4.6	6.42	2.5	1.97	0.6
Year 4 (2007)	Summer	Unprepared													
			never	49.07	2.5	1.23	0.2	1.73	1.0	7.47	3.6	8.69	4.1	0.94	0.5
			years 2+3+4	49.55	0.7	1.38	0.1	0.90	0.5	3.51	3.2	6.84	2.9	1.29	0.4
		Light disk trenching													
			years 2+3+4	48.61	0.9	1.38	0.2	1.21	0.3	7.52	3.6	5.74	2.2	1.12	0.4
		Heavy disk trenching													
			years 2+3+4	49.30	1.1	1.49	0.2	1.10	0.3	8.09	2.9	4.72	1.7	1.21	0.5
		Harrow													
			years 2+3+4	48.35	0.5	1.55	0.2	1.71	0.3	8.09	1.7	9.19	2.8	1.22	0.3
		Mounding													
			never	49.07	2.4	1.29	0.1	1.31	0.5	7.61	2.1	7.71	2.9	1.30	0.6
			years 2+3+4	50.02	1.7	1.65	0.3	1.40	0.3	7.36	3.6	5.88	2.0	1.44	0.4
	Spring	Unprepared													
			never	48.92	0.8	1.72	0.1								
			years 2+3+4	49.01	1.6	1.95	0.3								
		Light disk trenching													
			never	47.97	0.7	1.58	0.4								
			years 2+3+4	48.71	0.8	1.84	0.2								

	Heavy disk trenching					
		never	48.10	3.2	1.63	0.2
		years 2+3+4	48.66	1.1	1.99	0.1
	Harrow					
		never	47.85	1.5	1.63	0.2
		years 2+3+4	47.82	0.6	2.00	0.1
	Mounding					
		never	48.22	1.4	1.81	0.2
		years 2+3+4	49.10	0.5	2.27	0.2
Fall	Unprepared					
		never	51.36	0.5	0.44	0.0
		years 2+3+4	50.17	1.3	0.52	0.1
	Light disk trenching					
		years 2+3+4	50.27	1.1	0.52	0.3
	Heavy disk trenching					
		years 2+3+4	50.72	1.5	0.48	0.1
	Harrow					
		years 2+3+4	49.86	0.8	0.43	0.1
	Mounding					
		never	50.43	1.9	0.39	0.0
		years 2+3+4	49.39	0.9	0.46	0.1

Table A.4 Soil analyses of year 2 (2005). Methods of sampling and analysis are described in chapter II. Values are means from 8 sites; SD = standard deviation. Empty cells indicate that the analysis was not done for that sample. Fe and Al were analysed both with a pyrophosphate extraction (as indicated by "pyro" in brackets) and with a $BaCl_2$ extraction.

Treatments		C		N		C/N		Texture						Fe (pyro)		Al (pyro)	
								Sand		Silt		Clay					
Soil Preparation	Vegetation Control	%	SD	%	SD		SD	%	SD	%	SD	%	SD	%	SD	%	SD
Unprepared																	
	all	1.90	1.4	0.085	0.06	19.89	21.3	69.22	5.0	25.78	5.1	5.00	3.0	0.35	0.2	0.45	0.3
	never	1.76	1.1	0.079	0.05	22.67	1.7	69.38	3.6	25.63	4.3	5.00	4.4	0.36	0.3	0.40	0.3
	year 3	1.64	1.0	0.076	0.05	7.50	39.0	69.06	6.8	25.94	6.6	5.00	1.0	0.34	0.1	0.49	0.2
	year 2+4	1.72	1.4	0.074	0.07	28.40	8.8										
	years 2+3+4	2.55	2.1	0.115	0.08	21.56	2.7										
Light disk trenching																	
	all	1.77	0.8	0.079	0.04	22.90	2.7	73.91	8.6	21.56	8.1	4.53	2.1	0.31	0.3	0.39	0.2
	never	1.85	0.7	0.086	0.04	21.92	1.6	73.75	9.9	20.83	8.5	5.42	1.4	0.49	0.3	0.54	0.3
	year 3	1.72	0.7	0.076	0.03	22.46	1.8	74.00	8.9	22.00	8.8	4.00	2.4	0.20	0.2	0.30	0.2
	year 2+4	1.74	1.0	0.076	0.04	23.18	2.6										
	years 2+3+4	1.76	0.8	0.079	0.05	24.05	4.0										
Heavy disk trenching																	
	all	1.55	0.9	0.071	0.05	24.13	5.3	69.22	11.2	26.41	10.7	4.38	1.6	0.17	0.1	0.33	0.1
	never	1.54	0.6	0.070	0.03	22.88	2.9	80.63	6.2	15.63	6.2	3.75	0.0	0.13	0.1	0.29	0.1
	year 3	1.64	0.9	0.079	0.05	22.82	5.2	65.42	10.0	30.00	9.5	4.58	1.9	0.19	0.2	0.35	0.2
	year 2+4	1.38	0.8	0.059	0.04	26.61	7.7										
	years 2+3+4	1.65	1.3	0.076	0.07	24.19	4.4										
Harrow																	
	all	2.35	1.1	0.104	0.05	23.02	2.2	66.88	9.2	27.81	8.9	5.31	1.3	0.40	0.2	0.56	0.2
	never	2.52	1.2	0.112	0.05	22.54	1.1	70.00	3.5	24.38	2.7	5.63	0.9	0.33	0.3	0.46	0.2

	year 3	2.44	1.0	0.108	0.05	23.12	3.0	65.83	10.5	28.96	10.1	5.21	1.5	0.42	0.1	0.59	0.2
	year 2+4	2.21	1.4	0.093	0.06	24.34	2.0										
	years 2+3+4	2.25	1.0	0.103	0.05	22.00	1.9										
Mounding																	
	all	1.29	0.9	0.055	0.04	30.35	19.7	72.34	4.7	21.88	4.6	5.78	2.1	0.27	0.2	0.34	0.3
	never	1.76	1.3	0.076	0.06	26.40	6.2	70.63	0.9	22.50	0.0	6.88	0.9	0.32	0.2	0.61	0.4
	year 3	1.05	0.5	0.041	0.02	26.56	4.0	72.92	5.3	21.67	5.5	5.42	2.3	0.25	0.2	0.25	0.2
	year 2+4	1.19	0.7	0.053	0.04	29.54	16.9										
	years 2+3+4	1.18	0.8	0.050	0.04	38.88	35.5										

Treatments		pH (H_2O)		pH ($CaCl_2$)		K		Ca		Mg		Na	
Soil Preparation	Vegetation Control		SD		SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD
Unprepared													
	all	4.10	0.2	4.21	0.4	0.047	0.04	1.19	1.6	0.127	0.15	0.032	0.01
	never	4.07	0.3	4.11	0.6	0.038	0.03	1.92	2.9	0.166	0.22	0.028	0.01
	year 3	4.13	0.2	4.32	0.1	0.038	0.03	0.76	0.6	0.090	0.08	0.035	0.01
	year 2+4					0.038	0.02	0.94	1.2	0.103	0.12	0.030	0.01
	years 2+3+4					0.076	0.07	1.25	1.0	0.158	0.16	0.036	0.01
Light disk trenching													
	all	4.12	0.2	4.32	0.3	0.036	0.02	1.85	4.1	0.158	0.33	0.030	0.01
	never	4.18	0.2	4.37	0.1	0.040	0.01	0.60	0.6	0.062	0.04	0.030	0.01
	year 3	4.09	0.2	4.29	0.4	0.039	0.01	2.39	3.8	0.288	0.54	0.034	0.01
	year 2+4					0.035	0.02	2.67	6.6	0.160	0.33	0.025	0.01
	years 2+3+4					0.030	0.02	1.72	3.7	0.122	0.22	0.028	0.01
Heavy disk trenching													
	all	4.12	0.2	4.44	0.1	0.035	0.03	1.02	2.3	0.072	0.12	0.026	0.01
	never	4.00	0.2	4.45	0.2	0.030	0.01	0.66	1.0	0.059	0.06	0.026	0.01

	year 3	4.16	0.2	4.44	0.1	0.045	0.05	1.31	3.1	0.077	0.15	0.027	0.01
	year 2+4					0.031	0.01	0.60	1.1	0.046	0.06	0.025	0.00
	years 2+3+4					0.034	0.02	1.50	3.3	0.105	0.18	0.025	0.01
Harrow													
	all	4.14	0.2	4.29	0.2	0.042	0.02	2.30	4.9	0.165	0.26	0.031	0.01
	never	4.27	0.2	4.47	0.1	0.034	0.01	1.38	1.4	0.109	0.08	0.031	0.01
	year 3	4.10	0.2	4.23	0.1	0.051	0.03	1.89	2.7	0.159	0.17	0.032	0.01
	year 2+4					0.038	0.02	2.49	5.1	0.172	0.30	0.029	0.01
	years 2+3+4					0.045	0.02	3.32	8.0	0.212	0.41	0.032	0.01
Mounding													
	all	4.18	0.2	4.38	0.2	0.042	0.05	0.62	0.6	0.062	0.06	0.025	0.01
	never	4.19	0.3	4.32	0.1	0.051	0.04	0.66	0.7	0.055	0.05	0.025	0.01
	year 3	4.18	0.2	4.40	0.2	0.042	0.07	0.72	0.6	0.076	0.08	0.026	0.01
	year 2+4					0.039	0.04	0.53	0.4	0.055	0.05	0.023	0.00
	years 2+3+4					0.035	0.03	0.57	0.6	0.063	0.07	0.026	0.01

Treatments		Mn		Fe		Al		CEC		BS	
Soil Preparation	Vegetation Control	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	%	SD
Unprepared											
	all	0.0154	0.017	0.16	0.2	0.67	0.7	2.25	2.0	55.35	25.8
	never	0.0118	0.008	0.14	0.2	0.44	0.3	2.74	3.6	62.18	22.4
	year 3	0.0181	0.016	0.11	0.1	0.48	0.4	1.54	0.6	56.30	26.8
	year 2+4	0.0076	0.010	0.11	0.1	0.69	0.7	1.93	1.5	52.85	29.3
	years 2+3+4	0.0247	0.028	0.28	0.3	1.10	1.1	2.93	1.6	50.30	27.9
Light disk trenching											
	all	0.0127	0.027	0.13	0.1	0.60	0.6	2.81	4.3	50.78	26.2
	never	0.0087	0.008	0.19	0.2	0.87	0.8	1.81	1.2	40.49	16.3

	year 3	0.0278	0.050	0.13	0.1	0.57	0.6	3.49	4.1	56.20	33.6
	year 2+4	0.0048	0.004	0.09	0.1	0.38	0.3	3.37	6.9	53.00	25.3
	years 2+3+4	0.0095	0.016	0.12	0.1	0.57	0.4	2.60	4.0	53.41	29.1
Heavy disk trenching											
	all	0.0099	0.013	0.13	0.1	0.40	0.3	1.69	2.6	51.44	22.0
	never	0.0083	0.007	0.14	0.1	0.33	0.2	1.25	1.3	52.97	18.4
	year 3	0.0135	0.019	0.11	0.1	0.31	0.3	1.90	3.3	50.85	26.3
	year 2+4	0.0090	0.014	0.09	0.1	0.39	0.3	1.19	1.3	49.94	20.7
	years 2+3+4	0.0089	0.009	0.17	0.2	0.57	0.4	2.41	3.8	52.01	26.0
Harrow											
	all	0.0092	0.008	0.23	0.2	0.64	0.5	3.42	5.2	54.07	19.6
	never	0.0083	0.009	0.27	0.2	0.82	0.8	2.66	2.1	53.62	15.2
	year 3	0.0109	0.007	0.22	0.1	0.81	0.6	3.18	2.8	51.58	24.2
	year 2+4	0.0115	0.011	0.22	0.2	0.45	0.4	3.42	5.6	56.25	21.2
	years 2+3+4	0.0060	0.003	0.22	0.2	0.50	0.3	4.34	8.6	54.77	19.9
Mounding											
	all	0.0072	0.008	0.13	0.1	0.41	0.3	1.30	0.9	55.82	20.7
	never	0.0122	0.014	0.15	0.2	0.45	0.4	1.40	1.2	55.20	19.9
	year 3	0.0069	0.006	0.15	0.2	0.46	0.3	1.48	1.0	55.66	22.1
	year 2+4	0.0057	0.005	0.12	0.1	0.38	0.3	1.15	0.7	54.84	23.8
	years 2+3+4	0.0038	0.003	0.11	0.1	0.35	0.3	1.16	0.8	57.59	21.0

Table A.5 Soil analyses of year 4 (2007). One soil pit was dug per 1-ha plot and individual soil horizons were described, measured, and sampled for chemical analyses. Values are means from 8 sites; SD = standard deviation. Empty cells indicate that the analysis was not done for that sample. The B1 and B2 soil horizons represent the upper and lower sections of the B-horizon, respectively. DB was a sample from the B-horizon used to analyse texture and to calculate bulk density. Fe and Al were analysed both with a pyrophosphate extraction (as indicated by "pyro" in brackets) and with a $BaCl_2$ extraction.

Soil Preparation	Soil Horizon	C		N		pH (H_2O)		pH ($CaCl_2$)		Fe (pyro)		Al (pyro)		Sand		Silt		Clay	
		%	SD	%	SD	–	SD	–	SD	%	SD	%	SD	%	SD	%	SD	%	SD
Unprepared																			
	FH	2.23	2.7	0.22	0.2	4.74	0.3	3.96	0.3										
	Ae	2.71	1.3	0.45	0.5	4.54	0.2	3.75	0.2										
	B1	2.87	3.0	0.33	0.4	4.94	0.1	4.41	0.2	0.63	0.4	0.56	0.4						
	B2	4.27	5.4	0.59	1.1	5.11	0.1	4.67	0.3	0.26	0.2	0.39	0.2						
	C	15.70	17.0	0.65	0.6	5.10	0.2	4.70	0.3	0.17	0.2	0.59	0.4						
	DB	3.94	3.4	0.19	0.1	5.02	0.1	4.51	0.2					66.68	9.5	31.23	9.8	2.08	2.0
Light disk trenching																			
	FH	1.33	1.0	0.06	0.1	4.52	0.4	3.85	0.4										
	Ae	1.87	2.6	0.08	0.1	4.66	0.3	3.97	0.4										
	B1	13.62	18.1	0.50	0.7	4.99	0.1	4.52	0.3	0.33	0.2	0.62	0.6						
	B2	2.76	2.5	0.14	0.1	5.15	0.2	4.81	0.4	0.14	0.1	0.32	0.2						
	C	3.75	3.9	0.21	0.2	5.06	0.1	4.69	0.2	0.06	0.0	0.43	0.4						
	DB	8.96	16.6	0.41	0.7	5.04	0.1	4.57	0.3					66.52	9.8	28.90	16.2	4.58	8.2
Heavy disk trenching																			
	FH	6.40	13.4	0.34	0.6	4.47	0.2	3.77	0.2										
	Ae	1.06	0.5	0.12	0.2	4.44	0.3	3.78	0.2										
	B1	7.22	13.4	0.38	0.6	5.10	0.2	4.65	0.3	0.51	0.6	0.37	0.1						
	B2	6.45	8.3	0.33	0.2	5.07	0.2	4.75	0.3	0.29	0.5	0.26	0.1						
	C	1.29	0.9	0.16	0.2	5.11	0.1	4.84	0.1	0.12	0.1	0.30	0.2						

	DB	7.88	12.9	0.69	1 4	5.02	0.2	4.65	0.3					58.95	18.7	33.53	22.6	7.52	12.3
Harrow																			
	FH	9.88	16.9	0.35	0.6	4.92	0.5	4.29	0.6										
	Ae	3.21	2.4	0.14	0.1	4.65	0.2	3.96	0.3										
	B1	3.16	3.5	0.14	0.2	4.99	0.2	4.50	0.4	0.32	0.2	0.34	0.2						
	B2	7.89	17.7	0.26	0.6	5.10	0.2	4.68	0.4	0.18	0.2	0.30	0.1						
	C	4.61	5.8	0.21	0.3	5.18	0.1	4.73	0.3	0.09	0.1	0.57	0.6						
	DB	13.06	15.3	0.62	0.7	5.03	0.1	4.58	0.2					65.14	6.0	31.86	5.8	3.00	0.7
Mounding																			
	FH	8.97	13.0	0.48	0.5	4.50	0.4	3.75	0.4										
	Ae	1.19	1.3	0.44	0.8	4.33	0.3	3.56	0.3										
	B1	7.82	11.7	0.45	0.5	5.02	0.3	4.49	0.3	0.40	0.3	0.41	0.2						
	B2	0.78	0.5	0.04	0.0	5.20	0.2	4.82	0.2	0.10	0.1	0.21	0.2						
	C	7.34	10.7	0.20	0.2	5.26	0.2	4.83	0.2	0.06	0.1	0.32	0.2						
	DB	11.18	19.9	0.44	0.8	4.98	0.1	4.59	0.1					68.13	7.2	29.20	6.6	2.68	1.5

Soil Preparation	Soil Horizon	Bulk Density		K		Ca		Mg		Na		Mn		Fe		Al		CEC	
		g cm^{-3}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD	cmolc kg^{-1}	SD
Unprepared																			
	FH			0.071	0.02	0.29	0.2	0.045	0.03	0.68	1.0	0.002	0.002	0.062	0.11	0.54	1.1	41.23	26.2
	Ae			0.928	1.7	6.92	13.3	1.62	3.2	0.75	0.9	0.204	0.41	0.591	1.1	1.48	2.9	1.82	0.6
	B1			1.34	2.0	8.16	12.9	2.13	3.4	0.96	1.0	0.136	0.24	1.00	1.6	0.38	0.5	2.02	1.3
	B2			0.825	1.3	8.80	17.4	1.28	2.4	0.53	0.4	0.119	0.17	0.704	1.1	1.00	1 3	1.81	2.3
	C			0.354	0.60	1.70	2.8	0.358	0.64	9.6	20.9	0.129	0.27	0.096	0.13	6.27	12.3	2.46	3.0
	DB	0.86	0.3																
Light disk trenching																			
	FH			0.069	0.03	0.30	0.2	0.040	0.03	1.3	1.4	0.003	0.01	0.037	0.05	0.53	0.5	27.75	15.1

	Ae			0.410	0.60	5.37	9.0	1.00	1.7	0.16	0.1	0.078	0.14	3.39	5.8	0.85	0.7	3.35	1.9
	B1			0.630	1.1	3.05	4.4	0.907	1.5	0.98	0.9	0.059	0.08	1.92	2.8	1.33	2.5	3.66	3.4
	B2			0.921	1.3	8.83	14.2	1.69	2.6	2.5	2.2	0.120	0.18	1.31	2.8	1.00	0.9	1.44	1.4
	C			0.073	0.04	0.61	0.8	0.086	0 11	1.79	2.8	0.000	0.001	0.079	0.07	0.62	0.6	1.37	0.9
	DB	0.91	0.2																
Heavy disk trenching																			
	FH			0.071	0.04	0.60	0.5	0.064	0.05	0.37	0.3	0.001	0.00	0.028	0.05	0.27	0.3	25.20	11.4
	Ae			0.447	0.77	3.30	5.7	0.560	1.0	1.9	1.3	0.095	0.19	0.538	1.1	0.20	0.2	3.09	1.0
	B1			0.780	0.80	7.74	9.0	1.26	1.4	2.0	3.2	0.060	0.07	2.18	2.6	0.93	0.9	1.54	0 9
	B2			0.602	0.76	3.75	4.8	0.687	0.94	5.3	7.5	0.086	0.13	1.03	1.5	1.49	1.3	1.96	1.5
	C			0.068	0.02	0.59	0.7	0.184	0.31	0.50	0.5	0.001	0.003	0.042	0.05	0.32	0.4	1.33	0.9
	DB	0.90	0.1																
Harrow																			
	FH			0.061	0.03	0.33	0.2	0.049	0.04	0.87	1.2	0.002	0.00	0.055	0.08	0.40	0.6	27.27	17.3
	Ae			0.056	0.02	0.34	0.3	0.053	0.06	0.49	0.6	0.001	0.00	0.092	0.11	0.17	0.1	1 84	1.3
	B1			1.02	1.7	8.30	14.4	1.32	2.0	1.66	1.8	0.231	0.40	1.96	2.9	0.82	1.6	1.98	0.4
	B2			0.403	0.72	3.10	6.1	0.709	1.5	0.62	0.7	0.028	0.04	0.808	2.0	0.84	0.6	1.54	1.2
	C			0.356	0.59	5.03	10.3	0.602	1.2	1.06	1.2	0.138	0.31	0.166	0.09	2.07	3.7	2.70	1.4
	DB	0.72	0.4																
Mounding																			
	FH			0.084	0.04	0.34	0.2	0.060	0.05	0.81	0.6	0.003	0.00	0.032	0.05	0.98	2.1	39.92	27.2
	Ae			0.065	0.02	0.53	0.4	0.120	0.11	1.06	0.6	0.002	0.00	0.053	0.09	2.09	3.6	3.97	4.9
	B1			1.11	0.94	12.85	15.0	1.78	1.7	12.1	20.7	0.124	0.13	0.784	1.1	4.76	11.1	4.56	4.7
	B2			1.02	1 4	6.95	9.9	1.49	2.3	0.73	0.8	0.130	0 22	0.643	1.2	1.88	3.2	2.18	1.3
	C			0.101	0.05	0.92	0.7	0.085	0.04	1.11	1.2	0.006	0.01	0.075	0.11	2.77	4.6	1.23	0.7
	DB	0.96	0.3																

Table A.6 Shoot and leaf characteristics of hybrid poplars and *Calamagrostis canadensis* grasses used for the pot experiment in chapter III.

Variable	Treatment					
	HETp-C	HOM-C	HETr-C	HETp-noC	HOM-noC	HETr-noC
Hybrid poplar						
Foliar C, mg g^{-1}	45.34	45.23	45.80	45.66	45.62	45.70
SD	0.9	1.7	0.9	0.9	0.9	1.2
Foliar N, mg g^{-1}	1.47	1.45	1.43	1.85	1.76	1.85
SD	0.2	0.4	0.2	0.2	0.3	0.3
Foliar P, mg g^{-1}	15.13	3.89	14.10	14.59	4.85	13.15
SD	19.6	0.7	19.3	18.3	1.2	17.3
Foliar K, mg g^{-1}	17.19	23.18	17.06	16.89	22.70	19.01
SD	10.4	3.2	9.5	9.2	2.6	9.6
Foliar Ca, mg g^{-1}	11.61	10.41	10.74	10.06	10.42	10.25
SD	2.3	2.5	1.5	2.2	2.4	1.9
Foliar Mg, mg g^{-1}	2.67	2.48	2.47	2.42	2.44	2.58
SD	0.4	0.5	0.5	0.4	0.4	0.4
Foliar Mn, mg g^{-1}	0.16	0.15	0.17	0.19	0.18	0.19
SD	0.0	0.1	0.0	0.0	0.1	0.0
Calamagrostis canadensis						
Height, cm	128.73	121.09	114.83			
SD	37.9	15.8	28.5			
Number of shoots	78.70	70.55	66.09			
SD	19.1	11.8	27.1			
Aboveground biomass, g	116.37	116.09	103.38			
SD	48.6	39.9	48.0			
Foliar C, mg g^{-1}	43.02	43.39	42.83			
SD	1.1	0.9	1.5			
Foliar N, mg g^{-1}	0.90	0.80	0.72			
SD	0.2	0.2	0.1			
Foliar P, mg g^{-1}	2.94	2.87	2.58			
SD	0.5	0.4	0.3			
Foliar K, mg g^{-1}	15.38	12.57	12.71			
SD	3.4	2.0	1.9			
Foliar Ca, mg g^{-1}	2.54	2.33	2.25			
SD	0.8	0.8	0.6			
Foliar Mg, mg g^{-1}	1.52	1.39	1.47			
SD	0.5	0.4	0.4			
Foliar Mn, mg g^{-1}	0.08	0.07	0.08			
SD	0.1	0.0	0.1			

Table A.7 Above- and belowground characteristics of the three hybrid poplar clones used in the pot experiment of chapter III. Values are means from 24 replicates (pots); treatments of competition and fertility are pooled. Clones: 915319 = *P. maximowiczii* × *P. balsamifera*; 3308 = *P. deltoides* × *P. nigra*; 3729 = *P. nigra* × *P. maximowiczii*. Root links: EE = external-external links; EI = external-internal links; II = internal-internal links.

Variable		Clones					
		3308		3729		915319	
		Mean	SD	Mean	SD	Mean	SD
Aboveground							
Height, cm		79.67	15.7	115.69	31.3	108.96	19.1
No of shoots		2.26	0.8	1.57	0.5	1.65	0.5
Shoot biomass, g		15.71	9.1	28.01	16.7	17.36	7.6
Foliar biomass, g		8.27	4.6	13.64	9.0	7.64	3.6
Specific leaf weight, g cm^{-2}		0.0061	0.0008	0.0065	0.0009	0.0058	0.0007
Foliar C, mg g^{-1}		45.05	0.9	45.65	0.5	45.99	1.4
Foliar N, mg g^{-1}		1.82	0.3	1.50	0.3	1.57	0.2
Foliar P, mg g^{-1}		11.93	15.6	11.58	16.9	9.85	14.8
Foliar K, mg g^{-1}		20.94	9.4	17.78	8.2	18.79	7.1
Foliar Ca, mg g^{-1}		10.23	1.2	8.41	0.9	12.82	1.2
Foliar Mg, mg g^{-1}		2.64	0.2	1.95	0.1	2.86	0.2
Foliar Mn, mg g^{-1}		0.18	0.0	0.12	0.0	0.21	0.0
Belowground							
Root biomass	pot total, g	17.51	14.8	21.33	18.9	10.77	8.4
	pot ratio	2.36	2.9	1.71	1.1	2.21	2.3
Root length	pot total, cm	5068	4223	5375	4985	3697	2510
	pot ratio	1.96	2.5	3.37	6.7	1.99	3.0
Root surface area	pot total, cm^2	1097	910	1272	1163	793	529
	pot ratio	1.96	2.4	3.27	6.2	1.99	2.6
Specific root length	pot total, g cm^{-1}	0.0034	0.0018	0.0041	0.0014	0.0029	0.0011
	pot ratio	1.56	1.5	1.12	0.6	1.18	0.8
RTRS	pot total, No tips cm^{-2}	10.62	4.8	9.32	2.9	9.81	1.7
	pot ratio	0.91	0.3	1.03	0.3	0.89	0.2
RBRS	pot total, No branches cm^{-2}	23.95	5.2	21.50	5.3	24.21	3.2
	pot ratio	0.97	0.2	1.07	0.2	0.99	0.2
Average length of EE links	pot ratio	1.13	0.3	0.94	0.2	1.01	0.2
Average length of EI links	pot ratio	1.07	0.2	0.97	0.2	1.05	0.2
Average length of II links	pot ratio	1.08	0.3	0.96	0.1	1.01	0.1
Average diameter of	pot ratio	1.07	0.3	1.00	0.1	0.96	0.1

EE links							
No of EE links	pot ratio	1.85	2.2	3.89	8.1	2.41	5.3
No of EI links	pot ratio	2.04	2.4	3.56	7.3	2.05	3.5
No of II links	pot ratio	2.53	3.4	4.02	8.8	2.37	4.0
Total no of root links	pot ratio	2.41	3.2	3.93	8.6	2.31	3.9
Root magnitude	pot ratio	1.97	2.3	3.64	7.5	2.13	3.9
Relative root magnitude	pot ratio	1.02	0.1	1.00	0.1	1.03	0.1

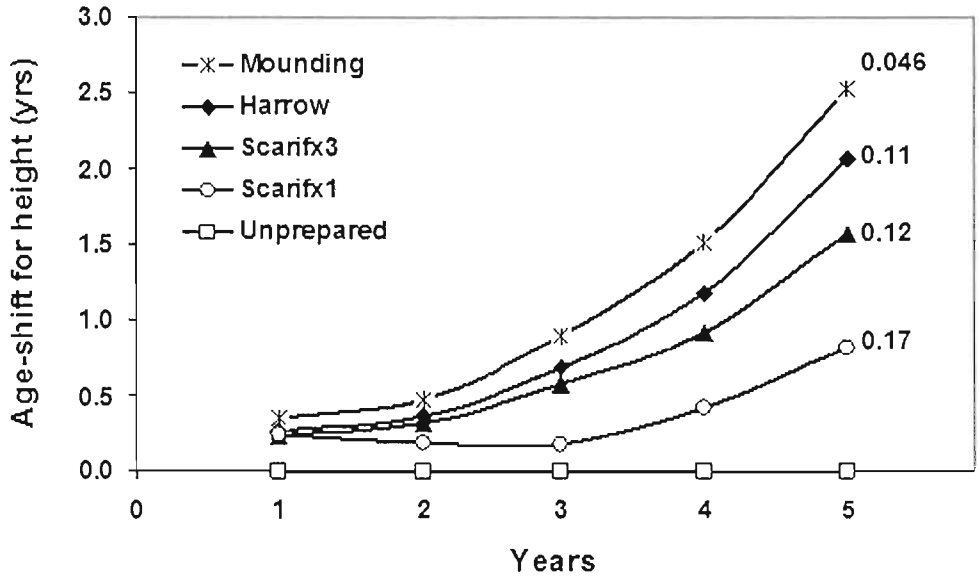

Figure A.8 Age-shifts for tree height, in years, for all mechanical soil preparation (MSP) treatments and for the first five years of growth (see chapter I). The "unprepared" control serves as a reference with which the other MSP treatments are compared, hence its age-shift values are set to zero. Probability that this control was significantly different from a given MSP is given by P-values adjacent to and at the right of age-shift curves.

Age-shifts were calculated by fitting linear regressions of cumulative annual height over time in order to construct height-age curves for all treatments (20 combinations of MSP x VC) at each site (n = 8). In the present case, this meant using the mean growth response in each 0.25-ha subplot. The slowest height growth (namely unprepared, unweeded or unfertilized plots) was then used as a reference and by substituting it in each height-age curve, it was possible to calculate at what age a treatment would have attained the same height as the reference, and thus how many years it was "shifted" over the timeline, or how many years of growth were gained by applying the treatments (i.e., the age-shift). This approach was used recently by Kimberley et al. (2004), South et al. (2006), and Carlson et al. (2008). It assumes that the shape of the height-age curves does not change over time in response to the treatments, only that they shift along the x-axis. Using linear regressions to build the height curves further assumes that growth varies linearly over time. Both assumptions were verified prior to calculations. Age-shifts over the first 5 years of hybrid poplar growth were compared through a mixed-effect REML analysis of variance using MSP treatments, VC treatments, and the interaction of MSP and VC as fixed effects, sites and plot as random effects, and accounting for auto-regressive correlation of rank one between years within a plot.

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